# The effects of landscape heterogeneity on arthropod communities in rice agro-ecosystems

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*"The natural world is the greatest source of excitement. The greatest source of visual beauty. It is the greatest source of so much in life that makes life worth living."*

- Sir David Attenborough

*"So important are insects and other land-dwelling arthropods that if all were to disappear, humanity probably could not last more than a few months."*

- E. O. Wilson

# Preface

I have always been drawn to nature with a particular interest in tropical ecosystems. After getting a Bachelor of Science in Biology of Organisms and Populations at Université Henri-Poincaré (UHP Nancy-1), I started an adventure unlike any other and decided to pursue my Master studying tropical ecology at the University of La Reunion in the Indian Ocean. My first research project led me to become familiar with the concept of biological control to reduce the presence of an invasive plant species (*Rubus alceifolius*). At the end of my master, I came back to the oceanic climate of Western France and studied the ecology of passerine birds in the salt pans of Guérande. There, I was introduced to landscape ecology and the identification of birds via sight and songs by Dr. Laurent Godet from the CNRS of Nantes. I have no doubt that studying alongside Laurent helped me find my calling. With a background in landscape ecology, I now use aerial images to better understand species-habitat relationships.

Accepting to work at the Helmholtz Centre for Environmental Research (UFZ) was the best opportunity at the right time since it was the perfect combination of my developed interests for landscape ecology, biological control and tropical ecosystems. Moreover, to my knowledge, no one had yet investigated the effects of landscape heterogeneity on arthropods in rice agro-ecosystems. Consequently, being part of this project felt like I would venture into the unknown. The study itself required a considerable amount of time in the Philippines to collect the data and identify the arthropods. Therefore, I spent more than 13 months as a guest scientist at the International Rice Research Institute in Los Baños to conduct my fieldwork, while immersing myself in a new culture. The Philippines is a unique and wonderful country where people showed me constant kindness and respect. Someone once said that first impressions are lasting ones. My first introduction to the Philippines started with a visit of the “eighth wonder of the world”, the rice terraces of Batad. These hand-carved rice terraces are a remarkable example of a cultural landscape that is believed to be 2,000 years old. However, rice production is facing multiple challenges and rice terraces are being abandoned by the younger generations for more attractive jobs in the cities.

The experience of living in a foreign country and culture can turn into the best stories, i.e. the simple discovery of a large Atlas beetle (*Chalocosoma atlas*), or witnessing the power of the typhoons Yolanda and Rammasun (and consequently living without electricity for two weeks), or just becoming unexpectedly addicted to video-karaoke. In the present thesis, I briefly introduce the importance of rice production and the multiple threats it is facing. The research experience at the Helmholtz Centre for Environmental Research in Leipzig allowed me to integrate GIS and remote sensing data, together with mixed-modelling approaches, to address the questions asked in the present thesis. More specifically, the findings provided a first insight of the effects of landscape heterogeneity in reducing herbivore pests and enhancing natural enemy populations in rice agro-ecosystems. As an integral part of the LEGATO project, the results of this thesis focused on sustainable solutions in rice for controlling pests and limiting the threat they impose to rice production. Being the first study to quantify the effects of landscape heterogeneity on rice-arthropods, I hope this thesis contributes to future research aiming at sustainable solutions for rice production such as ecological engineering.

# Acknowledgements

In this section I would like to express my sincere gratitude to those who have supported and helped me during the course of this PhD.

First of all, I am extremely grateful to my supervisors, Pr. Dr. Ralf Seppelt and Dr. Tomás Václavík for offering me this position. None of the contributions present in this thesis would have been possible without the support, the independence, and the trust that Ralf gave me through these years. I am profoundly grateful to Tomás for his clear guidance and assistance, his motivation, commitment and dedication, his encouragement, and understanding. It has been a privilege working with Tomás and I cannot stress enough how much I value your support as a colleague but also as a friend. My warm thanks to Pr. Dr. Josef Settele, the project coordinator of the BMBF Project LEGATO, who made this possible and for the friendly discussions and advice. My deep thanks to the wonderful people working at the CLE department at UFZ for providing the best working environment I could hope for. I would also like to thank the administrative staff at CLE, especially Sindy Bleiholder, Nora Eigenwill and Catharina Reul Jimenez, who have been excellent, professional and saved me more than I can count for from administration disaster.

During my long stay in the Philippines, I had the privilege to work with Dr. Finbarr Horgan. Thank you for all your help while I was at IRRI. Thank you for making me part of your research group. Thank you for the invaluable advice you gave me on research, rice, insects and politics! Thank you for making me improve myself! To all the people who helped me during the fieldwork, many thanks to all the helping hands! For the great stay and meals at Nature Mist, I want to thank Jesus Victor “Jappan” Bustamante and his family! For carrying the heavy equipment in the rice terraces, I want to thank my crew members Jerry and Raymond! For the help provided with the blow-vac, transportation, fieldwork and cooking, I want to thank Alberto Naredo, Vincent Vertrudes, Reyuel Quintana and Liberty Perez Almazan. For helping me with the identification of arthropods, I want to thank Sylvia “Bong” Villareal and Josie Lynn Catindig, but also Libby, Weng and Juvy. To all of you, maraming salamat po!

My deepest thanks to the wonderful people I met in the Philippines. First, thanks to Frederic, Anshuman and Elena for the great adventures we shared together! From Puerto Galera to Hongkong then Singapore, from the typhoons to ping(beer)-pong, from karaoke to "I did not order this", you made my stay in the Philippines so memorable. Many other people shared these amazing adventures as well and I would like to especially thank Jesus, Richard, Claire, Alex, Katharina, Adrian, Fatemah, Vu, Elsa, Jörn, and the international IRRI group. Special thanks to my Filipino friends whom I shared the best cultural experiences. Thank you, James, for the set-up, the "just one beer", the karaoke and our discussions at Elbi Square! Thanks also to Pia, Fame, Sly and of course Iza.

My warmest thanks to my friends in Germany! First, I would like to thank Stefan for his invaluable friendship! You have been a great support in my life as my translator and my friend. A big thanks to the super heroes: Captain Obvious, Energy man and the Nerdinator! Thank you all for the best experience I could hope for! Thank you for the good times, the movie nights, the ski-trips, the Berlin trip (let's forget about that one), the excursions, the discussions, but most of all thank you for helping me keep my sanity during these years. Thank you, Stefan, Micha, Seb, Karla, Frederic (again?), Ameur, Cheng, Andreas D. and Johannes.

J'aimerais également prendre le temps de remercier, de tout mon coeur, ma famille, pour votre soutien et votre écoute durant toutes ces annèes. Oui, c'est enfin fini! Merci pour votre aide, votre attention et de m'avoir suivi dans mes choix professionels. Cela n'a pas toujours été facile et la distance n'a pas beaucoup aidé. Votre encouragement et les brefs moments partagés ensemble ces dernières annèes me sont très cher. Merci pour tout!

Finally, I would like to thank the most incredible person I have ever met during this adventure, my wife Arriza. I want to thank you for your patience, your support and your love. From the Philippines to France and Germany, your presence has been the most precious gift. Mas mahal kita!

# Abstract

Irrigated rice croplands are among the most biologically diverse agroecosystems globally. However, this biodiversity is threatened by agricultural intensification and homogenization of farmed areas, resulting in a degradation of ecosystem services such as natural pest regulation. While evidence exists that increasing landscape heterogeneity in some agroecosystems can enhance natural enemy populations and promote bio-control, little is known about the multi-scale effects of landscape composition and configuration on arthropod communities in rice agroecosystems. In this thesis, I examined the influence of landscape heterogeneity on the distribution of arthropods in three rice-production regions in the Philippines and derived practical recommendations to improve biodiversity and biological control in rice production systems. Through the different chapters of this thesis, I measured landscape heterogeneity at different levels of complexity and spatial scales, and tested its effect on different types of the arthropod biodiversity (taxonomic and functional diversity).

In the introductory chapter, I discussed the ecology and importance of rice agro-ecosystems. Moreover, I addressed the main problems occurring for the past 50 years regarding pest damage in rice agriculture. Finally, I considered the potential benefits of landscape heterogeneity in enhancing natural enemies' populations and reducing herbivore pests.

The second chapter presents the general methodology used in the following chapters to measure landscape heterogeneity. Landscape heterogeneity was quantified via the calculation of landscape metrics or visual interpretation of remote sensing data. Additionally, I described the two sampling methods used to collect the arthropods in the fields (i.e. sweep net and blow-vac) and the different approaches to measure the diversity of arthropods.

The third chapter describes the arthropod composition in the three regions in the Philippines. Using a visual approach to describe landscape heterogeneity, I found no effect of fine-scale landscape heterogeneity on assemblage structure. Elevation gradient, used as a proxy for regional-scale effects in the study regions, explained more than 60% of variance in assemblage structure, suggesting that regional-scale effects rather than fine-scale landscape heterogeneity explained the composition of rice-arthropod communities in landscapes.

The fourth chapter demonstrates how landscape heterogeneity affected species abundance and species richness of rice arthropods. While predator abundance was solely driven by the availability of prey, all other functional groups in the rice-arthropod community were significantly affected by the composition and configuration of surrounding landscape features.

The fifth chapter highlights the role of landscape heterogeneity as an ecological filter of rice arthropods in relation to particular functional traits (i.e. dispersal ability, functional groups, and favored vertical stratum). I used different statistical analysis (RLQ analyses together with fourth-corner permutation tests) to study rice-arthropods traits across a landscape heterogeneity gradient. The findings of this chapter suggested that both the composition and configuration of the landscape can select or exclude species from the regional pool according to their functional traits.

The concluding chapter synthesizes the major findings highlighting the complex roles landscape heterogeneity plays in determining the arthropod community composition in rice agro-ecosystems. Moreover, I concluded that landscape composition can significantly reduce the presence of rice pests. The rice bunds provide an interesting prospect for ecological engineering applications as they can facilitate the movement of natural enemies and offer them additional shelter and food sources. In addition to landscape heterogeneity, rice arthropods responded to regional-scale effects, and predators displayed a strong numerical response to prey density.

As a perspective for further research, I discussed the limitations of the methods used in the thesis and the prospect of spatial and temporal heterogeneity studies to better understand arthropod composition in rice habitats.

The findings of this thesis are the first to quantify the effects of landscape heterogeneity on arthropods in rice agroecosystems. Therefore, this dissertation acts as a pioneer for further research, providing useful initial information for the enhancement of natural biological control at the landscape level.

### keywords

Biodiversity; Landscape heterogeneity; Macroecology; Trophic interactions; Pest control; Functional diversity; Species traits; Rice

# Zusammenfassung

Bewässerte Reisanbaugebiete gehören zu den biologisch vielfältigsten globalen Agrarökosystemen. Allerdings ist diese Biodiversität gefährdet durch landwirtschaftliche Intensivierung und monokultureller Verarmung von Anbauflächen, welche einen Abbau von Ökosystemleistungen, wie natürliche Schädlingsregulierung, nach sich ziehen. Während Nachweise zeigen, dass zunehmende Heterogenität der Landschaft von Agrarökosystemen zur Erhöhung von Feindpopulationen und Verbesserung biologischer Kontrolle führen kann, ist wenig bekannt über Multiskalen-Effekte von Landschaftzusammensetzung und -konfiguration auf Arthropodengemeinschaften in Reis-Agrarökosystemen. In dieser Dissertation untersuchte ich den Einfluss von Landschaftsheterogenität auf die Verteilung von Arthropoden in drei philippinischen Reisanbauregionen, um Empfehlungen für den Erhalt von Biodiversität und Verbesserung biologischer Kontrolle in Reis-Agrarökosystemen zu geben. In den verschiedenen Kapiteln der Dissertation, habe ich die Landschaftsheterogenität auf verschiedenen Skalen gemessen und deren Auswirkung auf die Arthropodendiversität (taxonomische und funktionelle Diversität) getestet.

In dem einführenden Kapitel diskutierte ich die Ökologie und Bedeutung von Reis-Agrarökosystemen. Zudem berücksichtigte ich die Hauptprobleme der letzten 50 Jahre, die in der Reislandwirtschaft durch Schädlingsbefall aufgetreten sind. Abschließend beleuchtete ich potentielle Vorteile der landschaftlichen Heterogenität, die zur Verbesserung der Populationen von natürlichen Feinden und Reduzierung von pflanzenfressenden Schädlingen führt.

Das zweite Kapitel stellt die allgemeine Methodik vor, die in den nachfolgenden Kapiteln verwendet wird, um Landschaftsheterogenität zu messen. Landschaftsheterogenität wurde quantifiziert durch die Berechnung von Landschaft Metriken oder visuelle Beurteilung von Luftaufnahmen oder Fernerkundungsdaten. Außerdem beschrieb ich die beiden Stichprobenverfahren die verwendet wurden um die Arthropoden direkt in den philippinischen Reisanbauregionen zu sammeln (d.h. Kehrnetz und Blow-Vac) und erklärte die verschiedenen Ansätze zur Messung der Diversität von Arthropoden.

Das dritte Kapitel beschreibt die Arthropodendiversität in den drei philippinischen Reisanbauregionen. Unter der Verwendung eines visuellen Ansatzes zur Beschreibung von Landschaftsheterogenität konnten keine Effekte feinräumiger Landschaftheterogenität auf die Assemblage Struktur gefunden werden. Ein Höhengradient, der als Proxy für regionale Effekte in den Untersuchungsregionen verwendet wurde, erklärte mehr als 60% der Varianz in der Assemblage Struktur. Dies legt nahe, dass eher regionale Effekte als feinräumige Landschaftsheterogenität die Diversität von Reis-Arthropoden-Gemeinschaften in Landschaften erklären. Im vierten Kapitel wird gezeigt, wie Landschaftsheterogenität Artenvorkommen und Artenreichtum von Reis Arthropoden beeinflusst. Während Raubtiervorkommen ausschließlich durch die Verfügbarkeit von Beute angetrieben wurden, wurden alle anderen funktionellen Gruppen in der Reis-Arthropoden-Gemeinschaft von der Zusammensetzung und Konfiguration der umgebenden Landschaftselemente signifikant beeinflusst.

Das fünfte Kapitel betont die Bedeutung der Landschaftsheterogenität als ökologischer Filter von Reis-Arthropoden bezüglich gewisser funktioneller Eigenschaften (d.h. Ausbreitungsfähigkeit, funktionelle Gruppen, und bevorzugte vertikale Schicht). Ich verwendete verschiedene statistische Verfahren (RLQ-Analysen zusammen mit der fourth-corner Permutationstests) um Reis-Arthropoden- Merkmale über einen Landschaftsheterogenitäts-Gradienten zu untersuchen. Die Ergebnisse der Untersuchung zeigen, dass sowohl die Zusammensetzung als auch die Konfiguration der Landschaft unter Berücksichtigung der funktionellen Eigenschaften von Arten das Artenvorkommen im Regionalen Pool beeinflussten.

Das abschließende Kapitel fasst die bedeutendsten Ergebnisse zusammen und betont die komplexe Rolle die Landschaftsheterogenität spielt in der Bestimmung von Arthropoden-Gemeinschaft in Reis-Agrarökosystemen. Weitere Ergebnisse wiesen darauf hin, dass die Komposition der Landschaft das Vorhandensein von Reisschädlingen signifikant reduzieren kann. Die Reisfeldbegrenzungen bieten eine interessante Perspektive für ökotechnische Anwendungen, da sie die Bewegung von natürlichen Feinden erleichtern können und ihnen zusätzlichen Schutz und Nahrungsressourcen zur Verfügung stellen können. Neben der Landschaft Heterogenität reagierten Reis-Arthropoden ebenso auf regionale Skaleneffekte. Räuber zeigten eine starke statistische Abhängigkeit von der Beutedichte.

Als Perspektive für weitere Forschung diskutierte ich die Grenzen der verwendeten Methoden in dieser Dissertation und Aussichten von räumliche und zeitliche Heterogenitäts-Studien Arthropodendiversität in Reislebensräumen besser zu verstehen.

Die Ergebnisse der Dissertation zeigen zum ersten Mal im wissenschaftlichen Kontext, die Auswirkungen von Landschaftsheterogenität auf Arthropoden in Reis-Agrarökosystemen. Die Dissertation ist somit wegbereitend für die Bereitstellung von ersten Informationen zur Verbesserung der natürlichen biologischen Kontrolle auf der Landschaftsskala.

### Schlüsselwörter

Biodiversität; Landschaftsheterogenität; Makroökologie; Trophische Wechselwirkungen; Schädlingskontrolle; Funktionelle Vielfalt; Arteneigenschaften; Reis

# Contents

# List of Articles

The following articles were published before submission of the dissertation and originate from work and results of this dissertation.

**Dominik, C.**, Seppelt, R., Horgan, F. G., Settele, J., & Václavík, T. (2018). Landscape composition, configuration, and trophic interactions shape arthropod communities in rice agroecosystems. *Journal of Applied Ecology*, https://doi.org/10.1111/1365-2664.13226

**Dominik, C.**, Seppelt, R., Horgan, F. G., Marquez, L., Settele, J., & Václavík, T. (2017). Regional-scale effects override the influence of fine-scale landscape heterogeneity on rice arthropod communities. *Agriculture, Ecosystems & Environment*, **246**, 269-278. https://doi.org/10.1016/j.agee.2017.06.011

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# Chapter 1

# General introduction

## 1.1 The importance of rice agro-ecosystems

Rice (*Oryza sativa* L.) is the daily diet of almost half the world's population (Maclean et al., 2002) and the staple food of nearly 3.5 billion people in the world (Muthayya et al., 2014). More than 90% of rice is grown and consumed in Asia alone (Maclean et al., 2002), while the rest is produced in Africa and Latin America. For most people living in Asia, rice is life (Gnanamanickam, 2009).

### 1.1.1 The origin, history, and ecology of rice production systems

Rice is a semi-aquatic annual grass plant that belongs to the genus *Oryza*, of which two species are domesticated and cultivated for human consumption: *Oryza sativa* and *Oryza glaberrima*. The first domestication of *O. sativa* originated in China and Southeast Asia between 8000 and 15 000 years ago (Huang et al. 2012; Molina et al., 2011). As of today, *O. sativa* is the most cultivated rice in the world, while the cultivation of *O. glaberrima* is confined to Africa (Seck et al., 2012; Muthayya et al., 2014). Although rice can grow in a wide range of environments, it grows faster, stronger and better in tropical areas.

There are three basic types of rice cultivation systems based on different crop management practices that have sustained production over millennia: irrigated systems, rainfed environments, and deepwater (Bouman et al., 2007). Irrigated systems are mostly found in the lowlands and provide 75% of the world's rice production (Maclean et al., 2002). Irrigated rice is generally grown in flooded fields surrounded by terrestrial levees (bunds). Supplementary irrigation is necessary during the dry season, which helps produce two to three crops of rice in a year. Rainfed rice is grown in bunded fields that are submerged with rainwater during the cropping season. However, due to the unpredictability of rainfall, rainfed fields can be too dry or too wet, and more susceptible to abiotic stresses such as drought (Bouman et al., 2007). In the mountainous regions with steep terrain, rice is often grown using a terrace system. Rice terraces not only prevent soil erosion and landslides but also provide the fields with constant water, which are often beneficial for other water uses. Finally, deepwater rice is grown in flooded conditions with more than 50 cm of water deep from a few days to a few months (Catling, 1992). In both irrigated systems and rainfed systems, rice is usually raised in a seedbed and then transplanted into a main field kept under continuous (irrigated) or intermittent (rainfed) water conditions, which help control weeds and pests (Bouman et al., 2007). Before rice transplanting, farmers soak, plow and puddle the land (the process of land preparation) which promote a good environment for seed/soil contact. It takes around three to five months for the rice plant to grow from seed to mature plant, depending on the variety of the plant and environmental conditions. The growth of the rice plant is divided into three stages: (1) vegetative (germination to panicle initiation); (2) reproductive (panicle initiation to flowering); and (3) ripening (flowering to mature grain) (Figure 1.1.1).

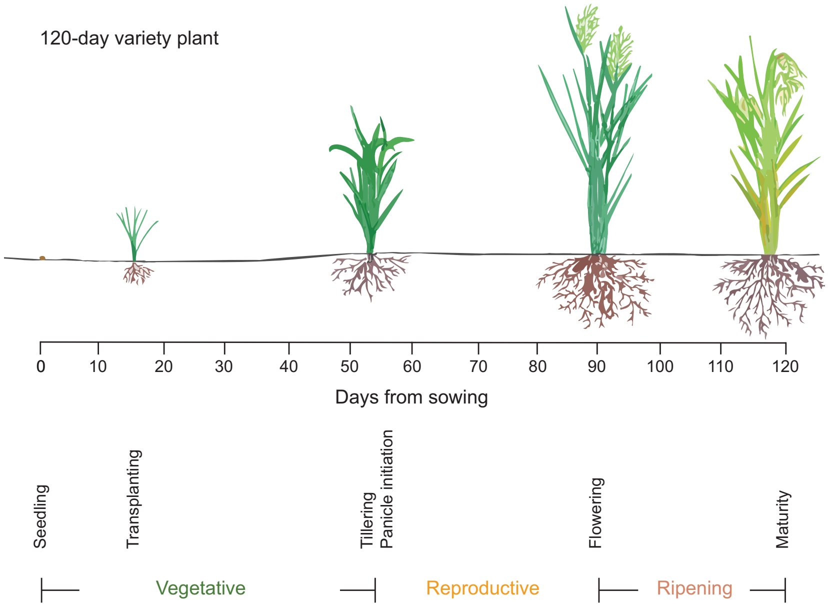


**Figure 1.1.1:** Growth stages of a 120-day variety rice plant (adapted from Bouman et al., 2007).

### 1.1.2 The Philippines case and food security

In the Philippines, rice is generally produced on small landholdings averaging 1.7 ha (Estudillo and Otsuka, 2006) and is the source of income and employment for about 12 million farmers and family members (Altoveros and Borromeo, 2007). Despite the consistent pursuit of a rice self-sufficiency policy since the 1950s (Habito and Valenzuela, 2016), the Philippines yet remain a major importer of rice. Like other countries that have been consistently importing rice (Indonesia, Sri Lanka, Japan, Korea, and Malaysia), the Philippines suffer from its geographical location, being an archipelago comprised of islands without any major river deltas like in Thailand and Vietnam (Dawe et al., 2006). However, several other factors such as high prices of agricultural inputs, the lack of mechanization, labor price, limitations on land ownership, and rising population may also have hindered the rice self-sufficiency policy (Timmer, 2012; Diagne et al., 2013; Dawe et al., 2006). As the current world population is expected to reach 9.7 billion by 2050 (United Nations 2015), the global rice demand will continue to grow in the next decade. Seck et al (2012) projected global rice consumption to rise from 439 million tons (milled rice) in 2010 to 496 million tons in 2020 and further increases to 555 million tons in 2035. In addition, rice agro-ecosystems are facing several biotic and abiotic stresses including climate change, land degradation and water scarcity, which are threats to rice production (Parry et al., 2004). Finally, rice production is also threatened by pests (i.e. rats, herbivores, etc.) that can cause direct damage to the plant. Farmers can lose an estimated average of 37% of their rice crop to arthropod pests and diseases every year (Savary et al., 2000). Food security, especially in the developing countries, is a critical issue. Thus, rice production is in urgent need to adopt new strategies if it is to survive and evolve.

## 1.2 Increasing rice production: Lessons from the past

To help ensure food security today and in the future, rice production must increase. This can only be met by increasing crop yields (agricultural intensification) or by expanding further areas for cultivation (agricultural expansion). In the past 50 years, rice agricultural techniques and systems have undergone major transformations. While spectacular progress was made in some areas, new problems arise in others.

### 1.2.1 The Green Revolution: progress and new threats

Before the Green Revolution changed tropical Asian rice in the 1960s, rice production was based on a low yielding traditional system that used rice landraces developed by farmers and produced with nominal artificial inputs (Bottrell and Schoenly, 2012). The Green Revolution bolstered food production and world food security via the introduction of high-yielding rice cultivars, controlled irrigation, synthetic fertilizers, and pesticides to farmers (Jennings, 1974). These new technologies quickly replaced traditional farming methods and significantly contributed in increasing rice production in many areas. New high-yield rice cultivars reached harvest maturity faster than traditional cultivars (105-110 days vs 160-200 days) which led to the appearance of large monocultures capable of growing two to three crops per year from the same rice field. Additionally, artificial fertilizers and chemical pesticides became predominant features of the new farming systems and were perceived as an insurance to increase yields and protect the crops (Bottrell and Schoenly, 2012). As a result, Philippines rice production increased an average of 12.4% each year from 1967-1968 to 1971-1972 (Jennings, 1974).

Ten years after the Green Revolution, nearly 70% of farmers planting new high-yielding rice cultivars regularly applied pesticides in their field (Kenmore, 1991), despite the fact that pesticide application was rarely necessary to increase rice production (Matteson, 2000). Advertised as a mean to avert disastrous pest losses, farmers continued to treat their crops with pesticide sprays at the wrong target or when pests were not even a problem (Heong et al., 1995). Recurring outbreaks of the brown planthopper (BPH), *Nilaparvata lugens* (Stal) (Hemiptera: Delphacidae), started to occur shortly after the introduction of the Green Revolution new technologies. BPH is an arthropod feeding on rice causing direct damage through the removal of large amounts of plant sap (Sogawa, 1982), and is a vector of several viruses to the plant (Cabauatan et al., 2009). When infestation levels are high, populations of BPH can cause the complete drying of the rice plant, a phenomenon called “hopperburn”" (Bae and Pathak, 1970). With the increase of hopperburns occurrences, the farmer’s fear of arthropod pests was reinforced and the need to apply more pesticides intensified (Heong et al., 1994; Bottrell and Schoenly, 2012).

Prior to the Green Revolution, outbreaks of BPH occurred infrequently and were considered a localized and rare event (Kenmore et al., 1984). In response to the new threat that BPH outbreaks presented to rice production systems, researchers around the globe were invited at an international conference to review and identify the problem (Bottrell and Schoenly, 2012). They concluded that the intensification of rice cropping during the Green Revolution had transformed the rice landscape, with the succession of monocultures over large areas facilitating BPH populations to reproduce and disperse, ultimately encouraging BPH outbreaks. Pesticides were also identified to aggravate the problem by killing natural enemies that regulated BPH’s populations (Kenmore et al., 1984; Horgan and Crisol, 2013).

### 1.2.2 The Integrated Pest Management program (IPM)

To help prevent BPH outbreaks and yield loss due to arthropod pests, the International Rice Research Institute (IRRI), with technical assistance from the Food and Agriculture Organization of the United Nations (FAO), launched a major rice integrated pest management program (IPM) in tropical Asia (Bottrell and Schoenly, 2012). This new program combined pest-resistant cultivars, fertilizer management, agronomic practices to enhance natural enemies' populations of pests, and a more prudent use of pesticides (Bottrell and Schoenly, 2012). Farmers trained with IPM practices learned ecological concepts about different arthropod pests and reduced insecticide application by 50 to 80% while sustaining or increasing the yield of their crop (Matteson, 2000).

However, despite the efforts of the IPM programs to reduce pesticides and promote environmental friendly methods (Kenmore, 1991; Heong and Hardy, 2009; Matteson, 2000), the use of chemical control resurfaced as a primary strategy for controlling arthropod pests in rice and increased in the early 2000s (Escalada et al., 2009; Bottrell and Schoenly, 2012). As a result, planthopper outbreaks in Asia became equal to or worse than those observed during the Green Revolution (Heong and Hardy, 2009).

### 1.2.3 Arthropods of rice: friends or foes?

With the resurgence of pest outbreaks, the continuous increase of chemical control use by farmers possibly emanates from the disbelief that all arthropods are harmful (Palis, 1998). In South-East Asia, not only smallholder farmers were largely unable to distinguish between common beneficial and harmful arthropods (i.e. pests), but less pesticide use was associated with a greater knowledge of the arthropod fauna (Schreinemachers et al., 2017).

Tropical rice agro-ecosystems are characterized by a mosaic of contiguous dry land and temporary flooded fields, offering a biologically diverse and dynamic environment for microbial (prokaryotes and eukaryotes), floral (algae and weeds), invertebrates (insects, spiders, mites, mollusks, crustaceans), and vertebrate populations to flourish during the different stages of the rice plant (Cohen et al., 1994; Settle et al., 1996; Schoenly et al., 1996). Inventories of rice flora and fauna accumulated through the years have helped ecologists and agronomists to better understand rice communities and the complex ecological relationships within the rice habitat (Heong et al., 1991, 1992; Settele, 1992; Catling, 1993; Simpson et al., 1993; Barrion and Litsinger, 1995; Schoenly et al., 1998). In rice ecosystems, arthropod herbivores (rice, non-rice, and phytoplankton feeders) coexist with a large complex of beneficial species comprised of predators, parasitoids, detritivores (scavengers on dead organic matter), and “tourists” (accidental or incidental taxa), which inhabit the soil, water, bunds, base and canopy of the plant (Settle et al., 1996; Schoenly et al., 1998) (Figure 1.2.1).

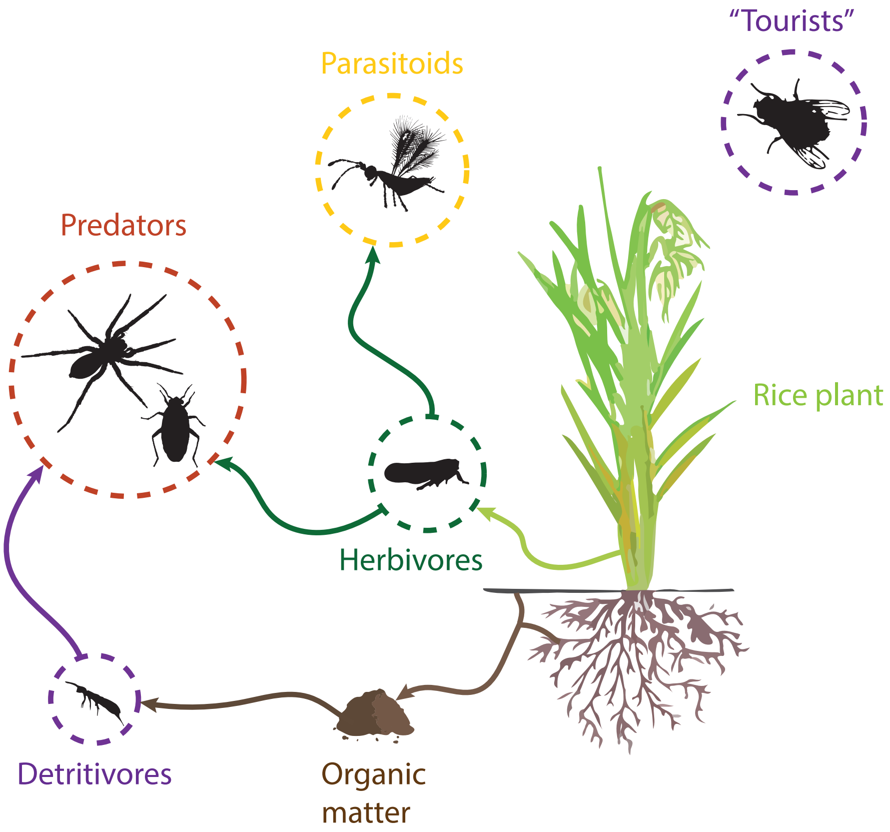


**Figure 1.2.1:** Simple representation of the trophic relationships of arthropods in the rice agro-ecosystems.

The rice agro-ecosystem is one of the most sustainable forms of agriculture (Kurihara, 1989), where invertebrates (mostly represented by arthropods) play a major role. For example, detritivores of rice can contribute to sustainable rice production by driving the release of nutrients from organic matter and promoting soil fertility (Schmidt et al., 2015). Almost half of the arthropods collected during a survey carried out in Sri Lanka (Bambaradeniya et al., 2004) consisted of predators and parasitoids, which are natural enemies of rice herbivores. The rich composition of natural enemies of pests in tropical rice agro-ecosystems (Heong et al., 1991; Ooi and Shepard, 1994; Schoenly et al., 1998) attests the high potential of natural biological control (Bambaradeniya et al., 2004). However, the overuse of pesticide applications can easily disrupt the predator-prey relationships and the food web structure, ultimately leading to the destruction of biodiversity and the reduction in the agro-ecosystem resilience to pest invasions (Heong et al., 1991; Cohen et al., 1994; Settle et al., 1996; Schoenly et al., 1998; Horgan and Cristol 2003).

## 1.3 Pest management at the landscape level

While the efforts of the IPM program were not enough, they revealed how pest management by chemical control is neither ecologically nor economically sustainable. In the United States, the benefits of natural enemies of agricultural pests are two-fold: they may offer a sustainable solution to pest problems, and the services they provide are high-valued ($13 billion per year) (Losey and Vaughan, 2006; Chaplin-Kramer et al., 2011). If natural enemies of tropical rice pests can indeed reduce the populations of herbivores to low levels, more emphasis should be put to fully understand the status and trends of arthropod diversity in rice agro-ecosystems. Can we identify the priorities as to their conservation and utilization as biological control agents?

### 1.3.1 Biological control: an important Ecosystem Service

The suppression of pests in agricultural crops via enhancement of natural enemy populations provides environmental and economic benefits since it can reduce yield loss without the negative environmental consequences linked to chemical control (Naylor & Ehrlich 1997; Pimentel et al.,1997). Hence, biological control is an important ecosystem service of great economic value (Naylor & Ehrlich 1997; Landis et al., 2008). For example, suppression of aphids by natural enemies has been demonstrated via experiments several times in different systems (Thies & Tscharntke, 1999; Thies et al., 2005; Rusch et al., 2013), and the value of its ecosystem service for soya bean aphids in the US was worth a minimum of $239 million in four US states in 2007-2008 (Landis et al., 2008). In tropical rice agro-ecosystems, the reduction of pesticides by 2/3 in Indonesia saved the government more than $100 million per year (1995 $US) (Gallhagher et al., 2009).

Biological control in agro-ecosystems is often supported and associated with biodiversity (Gurr et al., 2003). Enhancing agricultural biodiversity may favor pest management via the enhancement of the biological control function (Gurr et al., 2003). Natural enemies generally benefit from the composition and structure of the surrounding landscape and are found in higher abundance in complex landscapes as opposed to simple ones (Bianchi et al., 2006; Kremen et al., 2007; Chaplin-Kramer et al., 2011). Gurr et al. (2003) suggested that increasing biodiversity to enhance the biological control function may also result in a cascade of outcomes at other hierarchical levels, from the crop to the landscape level, potentially leading in an increase of several cultural services (aesthetic value of the landscape, cultural heritage, eco-tourism, etc.).

There is growing evidence that predators and parasitoids are key to regulating pest densities in rice agro-ecosystems (Kenmore et al., 1984; Schoenly et al., 1996; Settle et al., 1996). However, increasing the surrounding biodiversity does not always guarantee the suppression of pests (Gurr et al., 1998; Landis et al., 2000). Therefore, more emphasis should be put in understanding the complex interactions between pests, natural enemies, and the diversity of agricultural landscapes that surround them.

### 1.3.2 Applying landscape ecology for biological control services

The expansion of agricultural intensification worldwide has contributed to a rapid decline of biodiversity in agro-ecosystems (Robinson and Sutherland, 2002; Benton et al., 2003). Agro-ecosystems around the world differ widely in the amount of crop and non-crop habitats (i.e., landscape composition), and their spatial arrangement (i.e., landscape configuration) (Seppelt et al., 2016) (Figure 1.3.1). Together, these two components of the landscape describe the overall structure or heterogeneity of a landscape. How the different components of the landscape (composition and configuration) influence natural enemy diversity (Fahrig et al., 2011) at different scales are not fully understood (Batary et al., 2011). Multifunctional landscapes, which promote biodiversity and provide favorable conditions for agriculture based on ecological principles, may contribute to the development of productive yet sustainable agricultural systems (Bianchi et al., 2006).

Increasing the amount of non-crop habitats is generally associated with an increase in natural enemy diversity, because different habitat types may favor different natural enemy species (Bianchi et al., 2006; Gardiner et al., 2009; Chaplin-Kramer et al., 2011). In intensively managed crops, many species must be able to move between non-crop and crop habitats at the time of harvest or to colonize new fields at the start of the season (Wissinger, 1997). Non-crop habitats such as field margins or hedgerows are less disturbed than crop habitats, and can act as biodiversity reservoirs by providing additional sources of pollen and nectar, which are essential for many insects (Pickett and Bugg, 1998; Bianchi et al., 2006). Therefore, a more diversified agriculture landscape may harbor a broader diversity of natural enemies. However, positive relationships between natural enemy diversity and landscape composition provide no guarantee for effective pest control (Thies et al., 2005). Indeed, a few studies investigating multiple species frequently found positive relationships with landscape complexity for some species and negative or neutral relationships for others in the same system (e.g. Jonsen and Fahrig 1997; Letourneau and Goldstein 2001).

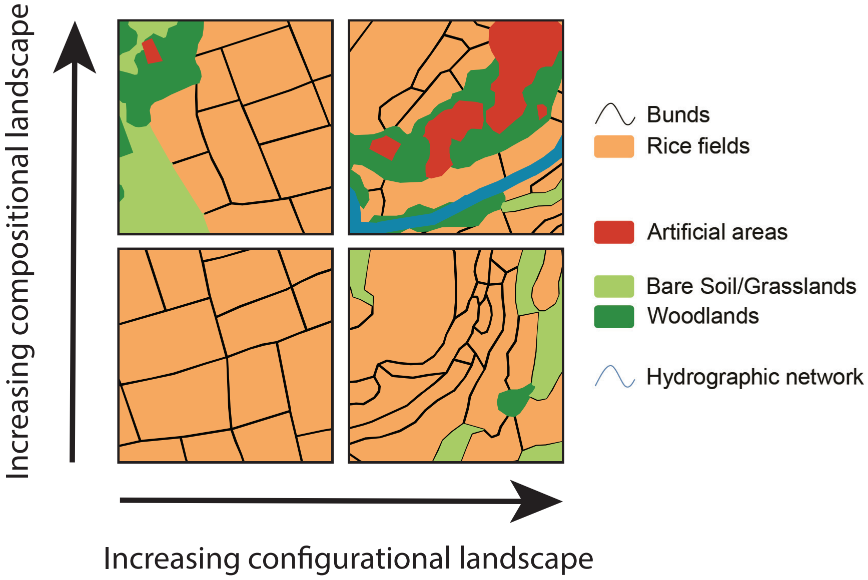


**Figure 1.3.1:** Landscape components of heterogeneity (adapted from Fahrig et al., 2011).

Landscape configuration describes both the spatial arrangement of different land-cover types and the shape of separate land-cover patches in the landscape. For example, small rice fields with irregular patches characterizing the rice terraces form a more complex configurational landscape than large and regularly shaped rice fields of intensified monocultures. In temperate agricultural landscapes, it has been shown that the abundance and diversity of parasitoid communities decrease with increasing distance from non-crop habitats, resulting in reduced parasitism (Tscharntke et al., 1998; Kruess and Tscharntke, 2000). In addition, natural enemy populations are more susceptible to habitat fragmentation and may act at smaller spatial scales than herbivores (Kruess and Tscharntke, 2000).

The spatial scale, distribution of crop and non-crop habitats, and configuration of the landscape may influence the natural pest control function in rice agro-ecosystems. However, to date, only a few studies have investigated the effect of landscape complexity on rice-arthropods in tropical Asia. Wilby et al. (2006) found that rice-arthropods composition differed at different stages of the rice plant. Rice near the flowering stage supported a greater arthropod diversity than other crop species (e.g., vegetables, fruits). Through the decades, many studies have debated on the optimum cropping pattern to adopt (Settle et al., 1996; Ives and Settle, 1997; Way and Heong, 2009; Schoenly et al.,2010). A synchronous cropping of the rice fields creates a rice-free fallow lasting a few months between the dry and wet season, whereas asynchronous cropping creates a mosaic of rice crops and temporarily unused fields (Litsinger, 2008). Synchronous cropping can promote the rapid increase in rice herbivore pests and produces smaller and less diverse predator populations than asynchronous crops (Settle et al., 1996). A prolonged fallow period following synchronous cropping can wipe out natural enemy populations and reduce the regulating services they are associated with (Bottrell and Schoenly, 2012). On the other hand, asynchronous cropping favors movement of predators migrating between fields, which can result in lower pest densities (Ives and Settle, 1997). Therefore, asynchronous cropping potentially creates continuous refuges for migrating arthropods (Bottrell and Schoenly, 2012). However, its deployment can result in less efficient use of irrigation water (Litsinger, 2008), whereas synchronous cropping offers a better conservation of water through the seasons.

The combined effects of landscape composition and configuration of rice agro-ecosystems are poorly understood at both the local and landscape spatial scales. However, there has been a growing interest in understanding how non-rice vegetation can promote the natural enemy populations in rice agro-ecosystems. In the face of agricultural intensification, recent studies are investigating the potential of new management practices, which aim at more sustainable rice-production (Gurr et al., 2003; Settele et al., 2008).

### 1.3.3 Ecological engineering: Toward new management practices

The term ecological engineering initially referred to “the environmental manipulation by man using small amounts of supplementary energy to control systems in which the main energy drives are still coming from natural sources” (Odum, 1962). The characteristics of ecological engineering are based on a limited use of chemical inputs and ecological principles (Gurr, 2009). Its application for pest management includes the use of cultural practices, usually based on habitat manipulation, to enhance the biological control function production with a landscape approach (Gurr et al., 2003). In contrast to simply increasing vegetation diversity to promote pest suppression, ecological engineering is a concept that emphasizes on precision where multiple potential plants are monitored and assessed to determine which ones are the best candidates to be introduced in the system (Gurr et al., 2004; Horgan et al., 2016). In rice agro-ecosystems, the concept is still young and early adaptations focused on integrating flower or vegetable strips along the rice bunds. For example, in field studies of Vietnam, growing nectar plants on the bunds significantly increased the number and impact of natural enemies on rice pests (Landis et al., 2010). New approaches such as ecological engineering have great potential for delivering ecosystem services and create healthy rice agro-ecosystems.

## 1.4 Research objectives and motivation

In the light of a changing world and the resurgence of old threats, research efforts should focus on developing sustainable management practices, switching investment of resources from modified crops (GM) and pesticides to refined ecological-engineering approaches (Settele et al., 2008).

In this thesis, I studied the effect of landscape heterogeneity on the biological control function in rice agro-ecosystems in the Philippines. The aim was to disentangle the effects of landscape composition and configuration on rice-arthropod communities at the landscape level. To my knowledge, no one had yet investigated the effects of landscape heterogeneity on the abundance and diversity of arthropods in rice agro-ecosystems, using a landscape ecology approach. Therefore, the following questions were answered in the present thesis:

1. What is the effect of fine-scale landscape heterogeneity and regional-scale drivers on rice arthropods? Is a binary description of the landscape heterogeneity adequate to identify responses from the rice-arthropod community?
2. How does the composition and configuration of the landscape affect the abundance and species richness of rice-arthropods? Are trophic interactions more important than the effects of landscape heterogeneity on the distribution of rice-arthropods?
3. How does landscape heterogeneity influence species traits of arthropods in rice agro-ecosystems?

# Chapter 2

# General Methodology

This thesis was conducted within the framework of the international and interdisciplinary project **LEGATO**, which stands for **L**and-use intensity and **E**cological En**G**ineering - **A**ssessment **T**ools for risks and **O**pportunities in irrigated rice-based production systems (Settele et al., 2015). The LEGATO project aimed to advance long-term sustainable development of irrigated rice fields, against risks arising from multiple aspects of global change via the quantification of the dependence of ecosystem functions and services generated in rice agro-ecosystems (Settele et al., 2015). The project's main objective was to investigate the interactions between rice agro-ecosystems, their surrounding landscapes and the human perception and valuation of relevant ecosystem services (Spangenberg et al., 2018).

## 2.1 Study sites of the Philippines

The Philippines is a country located in the western Pacific Ocean in Southeast Asia. It consists of an archipelago of about 7641 islands that are categorized broadly under three main geographical divisions from north to south: Luzon, Visayas, and Mindanao (Figure 2.1.1). All of the study regions are located on the main island of Luzon (Figure 2.1.1).

### 2.1.1 Research regions

To allow comparison of rice agro-ecosystems with different landscape structures, cultural identity, and landscape intensity, three 15 x 15 km areas (henceforth "region") were selected (Table 2.1.1 but see Appendix A for examples of each region). The three regions were: (i) a rice landscape in the hilly lowlands of

Laguna Province in southern Luzon (PH_1); (ii) an intensively cultivated rice landscape in Nueva Ecija Province (PH_2) situated in central Luzon; and (iii) a traditional terraced rice system in the mountainous Ifugao Province located in the north of Luzon (Figure 2.1).

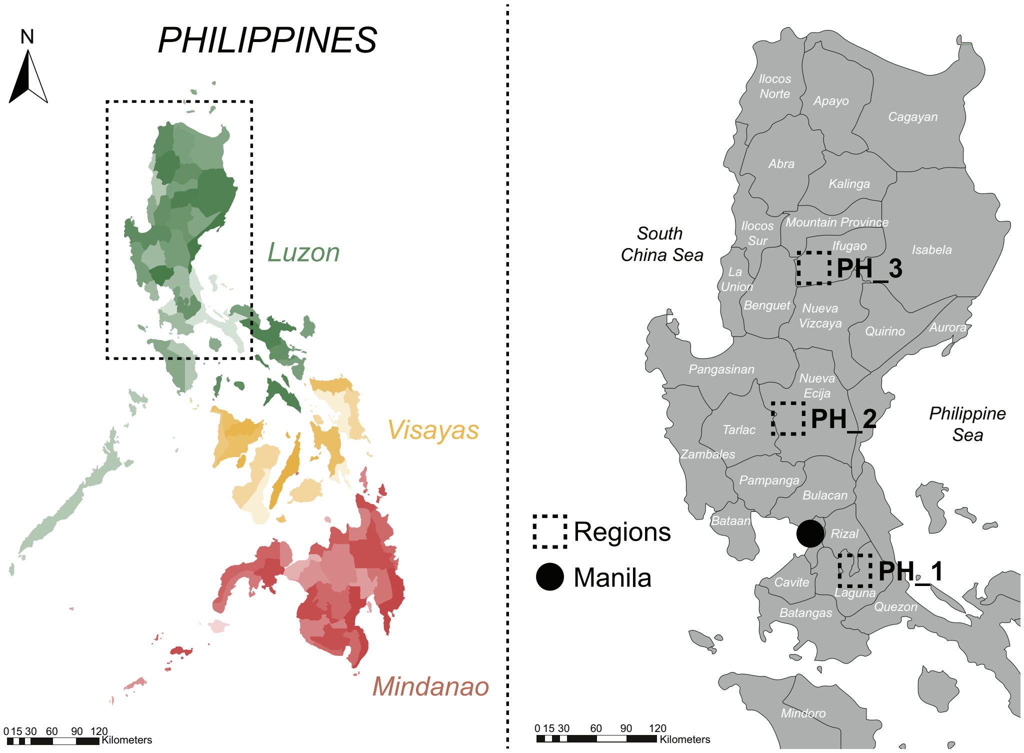


**Figure 2.1.1:** Study regions of the Philippines.

The Laguna Province (PH_1) is situated in southern Luzon, with study sites ranging in elevation from 25 m to 290 m asl. In these hilly lowlands, irrigated rice is double cropped, such that a standing rice crop including ratoon crops (where most of the plant is cut but roots are still intact, allowing fast recovery of the plant) is present during most of the year. Narrow plains and lightly undulating hills characterize the terrain. There are no remaining natural forests in the region, but agro-forestry is dominated by coconut plantations and other fruit trees.

The Nueva Ecija Province (PH_2) is located about 120 km north of Manila, in the Nueva Ecija Province of Central Luzon, at an altitude ranging from 45 to 60 m asl. This typical lowland region is characterized by flat relief with large monocultures of irrigated rice and only few semi-natural non-crop habitats. Rice is double cropped using comparably high levels of mechanization and agricultural inputs as in PH_1.

Finally, the Ifugao Province (PH_3) is located in the mountainous Ifugao Province, at an elevation ranging from 780 to 1300 m asl. Small rivers are commonly used as natural irrigation system for the characteristic rice terraces. The terrain is diverse and characterized by rice terraces that are believed to have existed for up to 2000 years. The region also includes large patches of primary and secondary forest habitats. Traditional rice varieties are cultivated with relatively low mechanization and few agricultural inputs, typically with one crop per year.

| **Region** | **Landscape structural diversity** | **Cultural identity** | **Crops per year** | **Mechanization** | **Chemical input** |
|---|---|---|---|---|---|
| Laguna (PH_1) | Medium | Low | 2 | Low: water buffalos, small hand tractors | High: Intensive use of pesticides and fertilizers |
| Nueva Ecija (PH_2) | Low-Medium | Low | 2 | Low: water buffalos, small hand tractors | High: Intensive use of pesticides and fertilizers |
| Ifugao (PH_3) | High | High | 1 | None: manual | None or low use of pesticides |

**Table 2.1.1:** Overview of the three research regions of the LEGATO project (based on Settele et al. 2013 and Tekken et al. 2017, adjusted).

### 2.1.2 Experimental design and core sites

Within the three studied regions, five pairs of rice fields (i.e. 10 “core sites”) were selected, according to the composition of the surrounding landscape, resulting in a total of 28 core sites (Figure 2.1.2). Indeed, field sampling could not be performed at two of the core sites in PH_2, because vegetables and not rice were grown at the time of sampling. The mean distance between two core sites within each pair was ~ 369 m and ranged from ~177 m to ~ 1192 m.

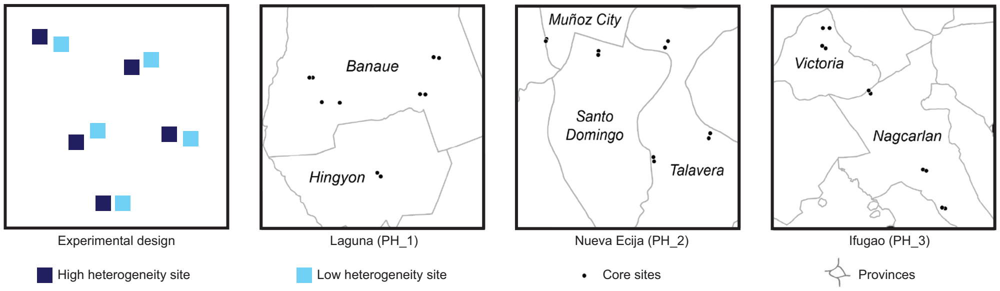


**Figure 2.1.2:** Experimental design and locations of the core sites within each region.

The core sites being relatively close to each other, they primarily differed in landscape heterogeneity within each region while other potential regional-scale effects were similar for each pair. For each site, landscape surface coverage and the proportion of rice fields within a 100 m radius were visually estimated by the same observer. Each pair of sites consisted of: (a) a rice field surrounded by high heterogeneity (i.e., the proportion of rice surrounding the core site was substantially lower than 50% with dominance of non-rice habitats including other crops, forests or settlements); (b) a rice field surrounded by low heterogeneity (i.e., more that 50% of the surface coverage consisted of rice fields and with little non-rice habitat) (Figure 2.1.3).

High heterogeneity site

Low heterogeneity site

**Figure 2.1.3:** Examples of high and low heterogeneity sites forming a pair in PH_1.

## 2.2 Measuring landscape heterogeneity

The compositional and configurational heterogeneity of the landscape are the two main components of landscape heterogeneity. They can be described and quantified by means of landscape metrics, using Geographic Information Systems (GIS).

### 2.2.1 Creating maps

All landscape features were identified and mapped within a 300-m radius around each sampling site using heads-up digitizing in a geographic information system (ArcGIS 10.3, ESRI) based on high resolution SPOT-5 DIMAP images (2.5 m). In addition, I collected ground-truth data in June 2014 to verify the photo-interpretation using Collector for ArcGIS (version 9.3, ESRI). I randomly attributed 10 ground-truth locations within each 300 m buffer, verified the land cover in the field and if necessary corrected the digitized maps.

Land cover features were classified at a consistent scale of 1:1000 into eight final categories: rice bunds, rice fields, plantations, artificial areas, bare soil/grasslands, woodlands, hydrographic network and ponds (Figure 2.2.1 but also see Appendix B, C and D).

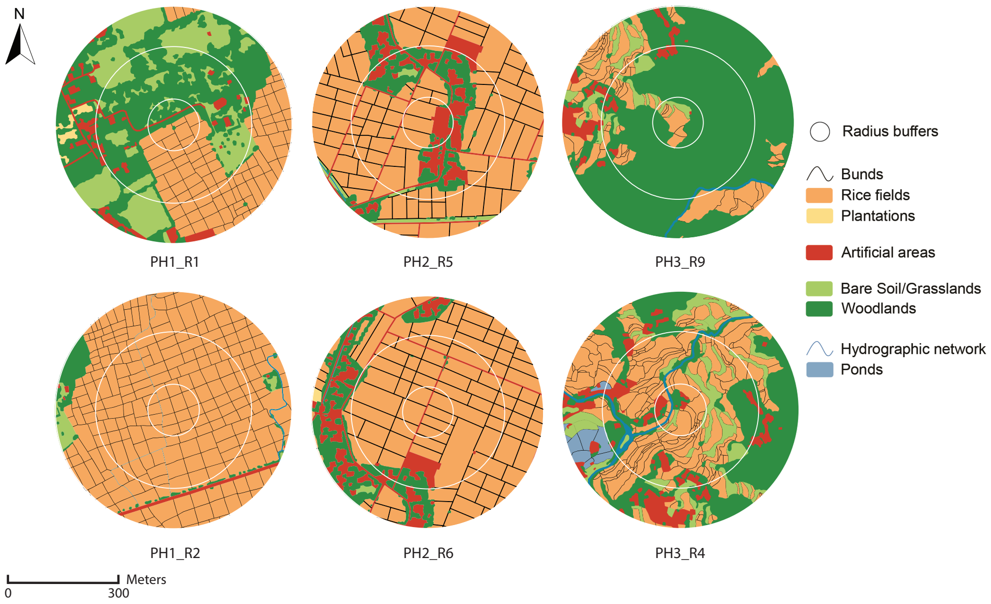


**Figure 2.2.1:** Examples of digitized maps for each region. High heterogeneity sites are represented on the top row. Low heterogeniety sites (associated paired to high heterogeneity sites) are represented on the bottom row.

### 2.2.2 Landscape metrics

Landscape metrics can be calculated at different levels to describe single landscape elements such as the size or shape of patches, or for whole landscapes by describing the arrangement of patches and composition of the landscape. In this thesis, I selected and calculated different metrics to best describe the landscape composition and configuration of the landscape using the software Fragstats 3.3 (McGarigal and Marks, 1995) (Table 2.2.1).

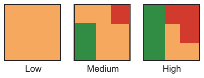
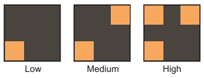
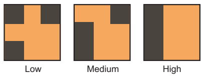
| **Landscape component** | **Description** | **Formula** | **Range** | **Graphical representation** |
|---|---|---|---|---|
| Landscape composition | Shannon's diversity index (SHDI) | $SHDI = -\sum_{i=1}^{m}(P_i * \ln P_i)$ | SHDI ≥ 0, without limit |  |
| Landscape configuration | Number of rice patches (NP) | $NP = n_i$ | NP ≥ 1, without limit |  |
|  | Physical connectedness of the rice bunds (COH) | $COHESION = \left[1 - \frac{\sum_{i=1}^{m} p_{ij}}{\sum_{i=1}^{m} p_{ij}\sqrt{a_{ij}}}\right]\left[1 - \frac{1}{\sqrt{A}}\right]^{-1}(100)$ | 0 ≤ COHESION < 100 |  |
|  | Shape complexity of the rice patches (FRAC) | $FRAC = \frac{2 * \ln(0.25 * p_{ij})}{\ln a_{ij}}$ | 1 ≤ FRAC ≤ 2 |  |
|  | Core Area Index of the rice patches (CAI) | $CAI = \frac{a_{ij}^{c}}{a_{ij}}(100)$ | 0 ≤ CAI <100 |  |

**Table 2.2.1:** Description of each landscape metric calculated in the thesis.

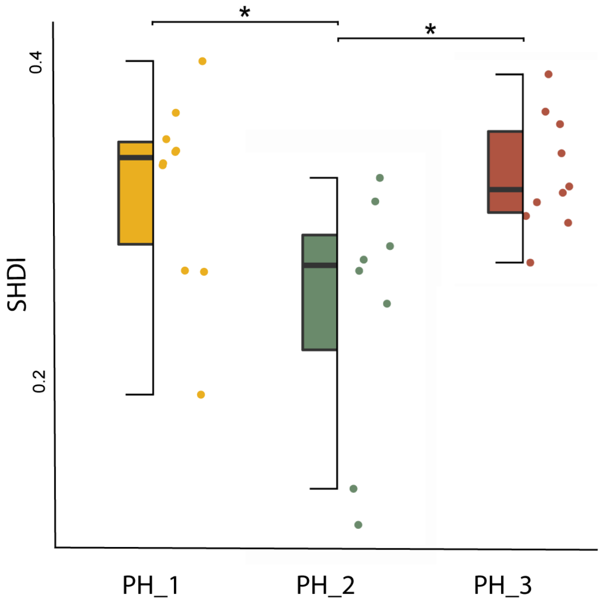


**Figure 2.2.2:** Box plots showing variations in landscape diversity (SHDI) between the three regions, with each core site represented as a dot. Line indicates the median, box shows the interquartile range (IQR) and the whiskers are 1.5 x IQR. Significant differences between regions are indicated by asterisks located next to the bar plots.

As a measure of compositional landscape heterogeneity, I used the Shannon's diversity index (SHDI) calculated at the landscape level with all eight land cover categories. Landscape diversity is generally perceived as a critical aspect of landscape heterogeneity, as many arthropods may be associated with a single land cover category (i.e. rice herbivores are mostly found in the rice habitat). I used a one-way ANOVA followed by a Tukey HSD post hoc test to compare landscape diversity between each region (Figure 2.2.2). The results indicated that landscape diversity significantly differed between PH_1 and PH_2, as well as between PH_2 and PH_3. However, landscape diversity did not significantly differ between PH_1 and PH_3, suggesting that these two regions shared a similar high landscape diversity.

The configurational landscape heterogeneity was measured exclusively for the rice habitat. The rice agro-ecosystem is usually composed of several rice fields (typically 1-3 ha in size) interconnected by a network of terrestrial levees (rice bunds). I calculated the number of rice patches (NP) as a measure of fragmentation of the rice habitat. Specifically, the fragmentation of the rice habitat (NP) involved the subdivision of contiguous large rice patches into numerous smaller patches. To quantify the structural connectivity of rice bunds, I calculated the patch cohesion index (COH) for the bunds. These terrestrial levees likely facilitate the dispersal of rice arthropods through the numerous rice patches. Rice terraces found in the mountainous regions (PH_3) are comprised of a mosaic of rice patches that greatly differed in size and shape. In contrast, monocultures of rice fields in the lowlands (PH_1 and PH_2) were often large and of rectangular shape to facilitate agriculture intensification. Thus, I calculated two different metrics to measure the shape complexity of rice patches. The shape of habitat patches may affect arthropod communities via edge effects, e.g. influencing host finding due to the way that plant odors are emitted from habitat patches (Stanton, 1983). First, I calculated a simple metric that described the geometric complexity of the rice patches (FRAC). Additionally, I calculated the core area index (CAI) for each rice patch to quantify the percentage of the patch comprised of interior area (rice) based on a 1-m edge effect (bund). For example, a large rice patch of rectangular shape will have a higher core area index than a small rice patch of irregular shape. The CAI best isolates the configuration effect since it is more an edge-to-interior ratio like many of the shape metrics.

## 2.3 Arthropod sampling

Arthropods were sampled using two sampling methods: a sweep net method and a vacuum (blow-vac) method similar to the one described by Arida and Heong (1992). Previous studies have shown that the abundance of arthropods can significantly differ from one method to another (Heong et al., 1991; Schoenly et al., 1996).

Sampling for both methods was conducted in the center of each core site between 0700 and 1100 h, after morning dew was evaporated, which coincides with minimal activity of the arthropods. In irrigated rice fields, the composition of the terrestrial arthropod community changes with the development of the rice crop and between cropping seasons (Heong et al., 1991). Farmers in the Philippines usually produce two rice crops per year in the lowlands - one during the dry season (January to June) and one during the wet season (June to December) - but only one in the highlands (January-June). Therefore, to ensure consistency of sampling, the data collection was conducted during the dry season of 2013 in PH_1 and PH_2 and during the one-cropping season for 2014 in PH_3. Sampling was performed at the maximum tillering stage of the rice plant (50 days after transplanting) because this stage is generally associated with a maximum abundance of arthropods (Heong et al., 1991; Wilby et al., 2006).

**Figure 2.3.1:** Author with the sampling equipment used to collect rice arthropods in the company of crew members Jerry and Raymond, and a Banaue inhabitant. a) Sweep net; b) Blow-vac; c) Enclosure.

### 2.3.1 Blow-vac sampling

The blow-vac machine was operated by a gasoline-powered motor and may be used for more quantitative studies of arthropods in rice (Figure 2.3.1). I used a custom-built sampling enclosure of about 1 m side length that was placed over four rice hills to prevent any escape of mobile invertebrates. The suction time was prolonged until all organisms present inside the enclosure were collected by vacuum pressure into collection vials. Within each core site, five vacuum samples were taken randomly.

### 2.3.2 Sweep net sampling

The sweep net is a simple and inexpensive way to monitor the presence of a variety of arthropods (Figure 2.3.1). I used a standard canvas sweep net and performed thirty sweeps per sample at each core site while walking twice at a constant pace along a randomly established transect. To prevent the escape of collected invertebrates, the sweep net was twisted at the end, the invertebrates knocked to the bottom of the net and subsequently transported in a collection container.

### 2.3.3 Arthropod identification

Sampled invertebrates were preserved in 70% ethanol. Most insects were sorted, counted, and identified using a binocular microscope to species level (or morphospecies level when species level was not possible) based on Barrion and Litsinger (1994) (Figure 2.3.2); however, dipterans and collembolans, as well as arachnids were only identified to family level due to the morphological similarity at the preadult stages and the quality of samples. In addition, the arthropods were grouped into functional groups as follows: detritivores/tourists, predators, parasitoids and herbivores. The “detritivores/tourists” group was composed of detritivores and non-predatory species which have no direct association with the rice plant but which may be attracted to surrounding habitats (Moran and Southwood, 1982).

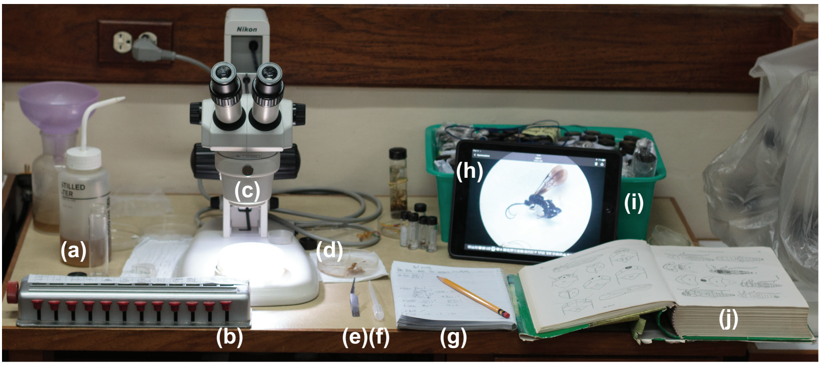


**Figure 2.3.2:** Equipment used for the identification of rice arthropods.

## 2.4 Methodological overview

The main objective of this thesis was to understand the responses of rice arthropods to the components of landscape heterogeneity. To answer the questions in **1.4.**, I measured landscape heterogeneity at different levels and scales, and tested its effect on multiple levels of the rice arthropod biodiversity through the different chapters.

### 2.4.1 Landscape heterogeneity: different levels and scales

In **Chapter 3**, I measured fine-scale landscape heterogeneity by comparing low and high heterogeneity sites as described in **2.1.2**. Selected within consistent frame conditions, I assumed that the low and high heterogeneity sites allowed a meaningful comparison of landscape heterogeneity and were also representative of the region in which they were sampled (Figure 2.4.1a).

In **Chapter 4**, landscape heterogeneity was quantified by calculating multiple landscape metrics. The influence of landscape heterogeneity on the rice arthropod was measured within each region and not globally across all three of them (Figure 2.4.1b).

Similarly, I calculated landscape metrics to describe the two main components of landscape heterogeneity in **Chapter 5**. However, the responses of rice arthropod to landscape heterogeneity was measured globally across all three regions (Figure 2.4.1c).

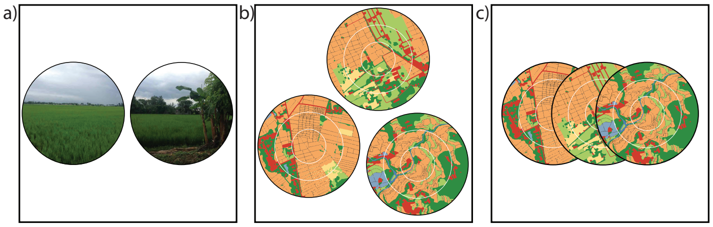


**Figure 2.4.1:** Different levels of landscape heterogeneity. a) High and low heterogeneity sites; b) Within each region; c) Across the three regions.

### 2.4.2 Measuring the biodiversity of rice arthropods

To better understand how the arthropod community responded to landscape heterogeneity, the rice arthropod biodiversity was measured at different levels through the chapters.

First, I described the arthropod community as a whole and identified potential assemblages across the regions (Figure 2.4.2.a). Additionally, I grouped the arthropods into functional groups, as described in 2.3.3. (Figure 2.4.2.b). I also tested the effects of landscape heterogeneity on the most common species found in the samples (Figure 2.4.2.c). Finally, I measured the rice arthropod biodiversity based on their functional traits (Figure 2.4.2.d).

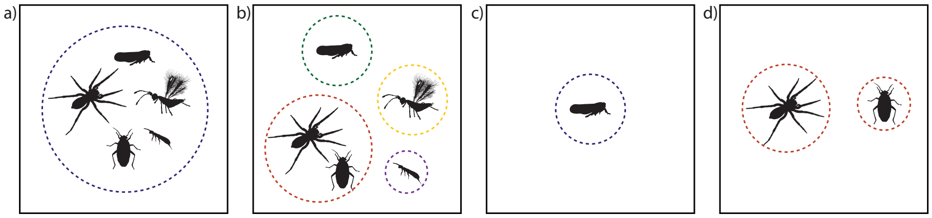


**Figure 2.4.2:** Different levels of arthropod biodiversity: a) Assemblages; b) Functional groups; c) Most common species; d) Species traits.

### 2.4.3 Outline

The present thesis is a compilation of chapters with the aim to better understand how rice arthropods responded to landscape heterogeneity. First, I started with a simple description of the landscape, then narrowed down the scales and levels of biodiversity and heterogeneity, and finally expanded to future research and perspectives (Figure 2.4.3).

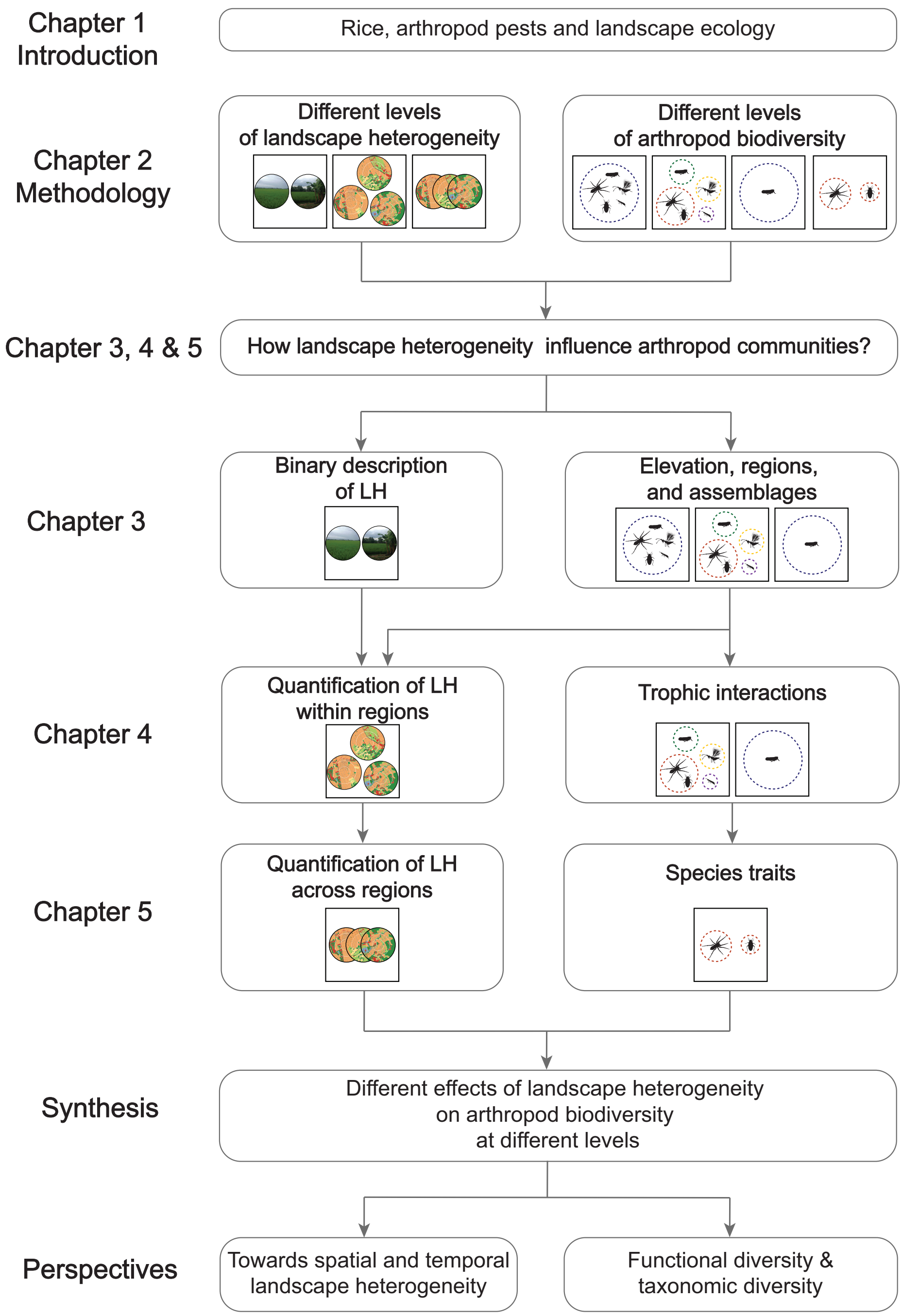


**Figure 2.4.3:** Methodological overview of the thesis showing the connections between each chapter (LH = Landscape heterogeneity). The illustrations within the diagram refer to Figures 2.4.1 and 2.4.2.

# Chapter 3

# Regional-scale effects override the influence of fine-scale landscape heterogeneity on rice arthropod communities

## 3.1 Introduction

Rice (*Oryza sativa* L.) is the main staple food for nearly half of the world's population (Zeigler and Barclay, 2008) and is among the most important cereal crops in the developing world (Seck et al., 2012). With the World's human population expected to reach 9.2 billion by 2050 (United Nations, 2015), the demand for rice continues to grow, exerting increasing pressure on rice production systems (Ericksen et al., 2009). Rice agro-ecosystems have been classified as human-made wetlands (Ramsar, 2010). Because of their alternate dry and wet conditions and their largely tropical distribution, rice fields have been associated with high biodiversity (Cohen et al., 1994; Settle et al., 1996). Rice production promotes complex landscape mosaics because contiguous dry land is often interspersed with the flooded rice fields. These landscapes can attract a wide range of aquatic animals and plants. For example, Schoenly et al. (1996) recorded more than 600 macroinvertebrate species in conventional-cropped fields in the Philippines, which surpasses that of most natural temperate systems (Pimentel et al., 1992). Such high levels of biodiversity support complex interactions among multiple organisms, which help suppress rice pests and diseases and thus enhance rice production via biological control (Altieri, 1999; Bottrell and Schoenly, 2012; Macfadyen et al., 2015). Although agro-ecosystems are designed and managed by man to provide provisioning ecosystem services such as food, forage and bioenergy (Kremen, 2005), they strongly depend on regulating ecosystem services such as pollination and biocontrol (Power, 2010). The latter is of particular importance in rice agro-ecosystems as pest damage is considered a major limiting factor (Pathak and Khan, 1994).

Agronomic intensification tends to reduce diversity in agro-ecosystems through the expansion of farmed land, the loss of field margin vegetation, and high intensity management on existing cropland (Swift et al., 1996; Robinson and Sutherland, 2002; Gerstner et al., 2014). This further leads to the simplification and homogenization of farmed areas, resulting in considerably fragmented semi-natural habitats (Robinson and Sutherland, 2002; Meehan et al., 2011) and a degradation of biodiversity and ecosystem services (Tscharntke et al., 2005). In most agro-ecosystems, monocultures are characterized by higher levels of pest damage and smaller populations of natural enemies (Power, 2010; Gardiner et al., 2009), whose abundance and diversity are negatively affected by the lack of potential food resources and habitats (Landis et al., 2000). Therefore, understanding the effects of landscape heterogeneity and other environmental drivers on the diversity of arthropod communities is crucial to sustainably manage rice production systems and the surrounding landscapes with a minimum harm to agro-biodiversity (Ericksen et al., 2009).

High landscape heterogeneity, i.e. the fine-scale composition and configuration of crop and non-crop areas, is generally associated with increases in natural enemy abundance and diversity (Thies and Tscharntke, 1999; Gardiner et al., 2009; Woltz et al., 2012). While the role of arthropod diversity in maintaining natural pest regulation is not yet universally accepted as a basic principle by farmers (Bianchi et al., 2006), the evidence that landscape heterogeneity improves biological control is mounting (Settle et al., 1996; Bianchi et al., 2006; Letourneau et al., 2009; Chaplin-Kramer et al., 2011). Complex landscapes with large amounts of semi-natural habitat may benefit arthropod communities by providing (i) refuge from agricultural disturbances (Meek et al., 2002; Kleijn and Sutherland, 2003; Coll, 2009), (ii) alternative hosts and prey or nectar resources, which are essential for many insects (Pickett and Bugg, 1998), and (iii) a moderate microclimate, which can promote the survival of, for example, parasitoids that experience shorter lifespans at temperature extremes (Dyer and Landis, 1996, 1997). Although the positive aspects of landscape heterogeneity have been explored across a range of cropping systems and study regions (O'Rourke, 2010; Chaplin-Kramer et al., 2011), little is known about their effects on arthropod communities in complex rice production systems. For example, Wilby et al. (2006) documented landscape impacts on the processes of community assembly in rice, largely through effects on abundance, but they found only weak and sometimes contradictory patterns concerning the impact of rice cover and landscape heterogeneity on arthropod diversity.

In addition to fine-scale landscape heterogeneity, rice arthropod communities are affected by climate, environmental conditions and other landscape and land use factors operating at a regional scale. Regional-scale drivers, such as elevation gradients, provide “natural experiments” for testing the distribution of insect biodiversity (K?rner, 2007; Samways, 2007). Elevation is often used as a surrogate variable for investigating the influence of regional climate conditions (Sanders et al., 2003), because both temperature and precipitation are highly correlated with elevation gradients. Temperature, in particular, plays a major role in the life history processes of arthropods (Sinclair et al., 2003), as it affects, among others, body growth and morphology, the number of instars and generations produced per year and the length of the life cycle (Hodkinson, 2005). In rice agro-ecosystems, the abundance of arthropods have been shown to decrease with increasing elevation but no significant trends were observed for species richness or diversity(Schoenly et al., 1996, 1998).

Whilst much emphasis has been placed in the past on describing the rice arthropod community itself (Heong et al., 1991, 1992; Settle et al., 1996; Schoenly et al., 1996, 1998), few studies so far have investigated the potential effect of fine-scale landscape heterogeneity or regional-scale effects on these communities. In this chapter, I examine whether fine-scale landscape heterogeneity is positively related to arthropod diversity, particularly the diversity of natural enemies, in tropical rice fields. To do this I examined arthropod community structure at sites with either fine-scale high or low landscape heterogeneity within a 100 m radius and along an elevation gradient in the Philippines. By including sites at different elevations, I could examine the relative contribution of regional-scale effects and fine-scale habitat heterogeneity in structuring the communities. Furthermore, I assessed the utility of two sampling methods for examining aspects of rice arthropod community ecology.

## 3.2 Material and methods

### 3.2.1 Study sites

The study was conducted in the three regions of 15 ? 15 km located on the island of Luzon in the Philippines as described in 2.1.1. To examine the influence of fine-scale landscape heterogeneity on arthropod community composition, five pairs of fields (i.e. 10 core sites) were selected within each region (see 2.1.2) according to the composition of the surrounding landscape, resulting in a total of 28 core sites. The core sites being relatively close to each other, they primarily differed in fine-scale landscape heterogeneity within each region while other potential regional-scale effects were similar for each pair. For each site, landscape surface coverage and the proportion of rice fields within a 100 m radius were visually estimated by the same observer (see 2.4.1a). Each pair of sites consisted of: (a) a rice field surrounded by high heterogeneity (i.e., the proportion of rice surrounding the core site was substantially lower than 50% with dominance of non-rice habitats including other crops, forests or settlements); (b) a rice field surrounded by low heterogeneity (i.e., more that 50% of the surface coverage consisted of rice fields and with little non-rice habitat). Selected within consistent frame conditions, I assume that the low and high fine-scale heterogeneity sites allow a meaningful comparison of landscape heterogeneity and are also representative of the region in which they were sampled.

### 3.2.2 Arthropod sampling

Arthropods were sampled using a sweep net method and a vacuum (blow-vac) method similar to the one described by Arida and Heong (1992) (see 2.3.1). Sampled invertebrates were preserved in 70% ethanol. Most insects were identified using a binocular microscope to species level (or morphospecies level when species level was not possible) based on Barrion and Litsinger (1994); however, dipterans and collembolans, as well as arachnids were only identified to family level due to the morphological similarity at the pre-adult stages and the quality of the samples. In addition, the arthropods were grouped into functional groups as follows: detritivores/tourists, invertebrate predators, parasitoids and herbivores. The "detritivores/tourists" group is composed of detritivores and non-predatory species which have no direct association with the rice plant but which may be attracted to surrounding habitats (Moran and Southwood, 1982).

### 3.2.3 Statistical analyses

#### 3.2.3.1 Characterization of the arthropod community

I characterized arthropod community structure as determined for each sampling method in each core site by calculating the abundance of all species, species richness (S) and the Shannon-Wiener index of species diversity (H'). To measure the differences in species structure among study sites, I performed non-metric multidimensional scaling (NMDS) ordinations after computation of a Bray-Curtis dissimilarity matrix based on arthropod abundances. The arthropod mean abundance data were square-root transformed prior to analyses, in order to reduce the influence of the most abundant species. As an additional test, I performed Ward's hierarchical cluster analysis of the Bray-Curtis dissimilarity matrix. Ward's algorithm is based on minimizing variances in hierarchically identified assemblages and performs well with aggregated data, for which the Bray-Curtis measure is generally recommended (Singh et al., 2010). The significance of the differences between arthropod assemblages derived from the Bray-Curtis matrix was assessed with a perMANOVA test. I also used a Mantel's test of spatial autocorrelation (based on a geographical distance matrix) to examine spatial dependence between study sites. Finally, I calculated the relative contributions of each species to the similarities within each assemblage using a SIMPER analysis, which examines the percentage contribution each species makes to the similarity within and dissimilarity between assemblages (Clarke et al., 1993).

In order to determine if the sampling method had an effect on the identified arthropod composition, I used a Mantel's test to examine the concordance between dissimilarity matrices constructed using data collected by each sampling method. In addition, I compared the total mean abundance (square-root transformed) of the 20 most common species (representative of each order) sampled by each sampling method using a one-way analysis of variance (ANOVA). I also used an unpaired t-test to compare rarefied species richness across all regions between the two sampling methods. The rarefaction method was used here as it standardizes the measure of species richness, accounting for potential bias from different sampling efforts or other factors that may lead to large differences in the number of collected individuals among samples (Gotelli and Colwell, 2010).

#### 3.2.3.2 Regional-scale effects and fine-scale landscape heterogeneity

In addition to distinguishing the two levels of landscape heterogeneity at sampling sites, I examined the effects of three basic environmental variables that are typical drivers of species distributions and community composition: elevation, mean annual temperature and mean annual rainfall (Atauri and de Lucio, 2001; Moreno-Rueda and Pizarro, 2007). The mean annual temperature and rainfall were both accessed from the CliMond archive at a resolution of 90 m (Kriticos et al., 2012). Elevation was obtained from the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global Digital Elevation Model (GDEM) v2 at a 30 m resolution (https://lpdaac.usgs.gov/). As elevation and climate conditions are often closely related, I used Pearson's correlation coefficients to test for multicollinearity among environmental variables (Appendix E). As their variability was high among regions but low within regions, these predictors can be potentially confounded with other factors specific to regions PH_1, PH_2 and PH_3 such as environmental variables or larger-scale landscape structure.

To examine the influence of regional effects on the arthropod assemblages derived from the Bray-Curtis dissimilarity matrix, I used the envfit function from the vegan package (R Core Team, 2016). This function calculates the goodness of fit statistics provided by the squared correlation coefficient as a measure of separation among the different levels of the variables. The significant factor with the highest fit was then plotted on the MDS (Oksanen et al., 2016).

I also examined the impact of regional-scale effects and fine-scale landscape heterogeneity on species abundance, richness and diversity. First, I assessed the variable effects on the total mean abundance (square-root transformed), total rarefied species richness and total species diversity for all samples across all study regions using a one-way ANOVA. As an alternative, I tested the same variables with a linear mixed effect model using “region” as a random effect. Second, I repeated the same analysis for the mean abundance (log transformed) of the morphospecies, which contributed the most to the similarities within each assemblage. Third, separately for each identified assemblage (PH_1-PH_3), I compared the abundance, richness and diversity measures between core sites with high and low levels of fine-scale landscape heterogeneity using a Student’s t-test. I performed this additional analysis separately for each assemblage, in order to avoid the potential effect of region and account for the lack of spatial independence.

Then I provided the same comparison between sites with high and low levels of fine-scale landscape heterogeneity for both the functional groups in each assemblage and for the morphospecies which contributed the most to the similarities within each arthropod assemblage using a Student’s t-test. Prior to statistical tests, I tested the normality of the data using the Shapiro-Wilk normality test. In the case of non-normal distributions, I used the Mann-Whitney tests instead of the t-tests. All statistical analyses were conducted in R version 3.1.1 (R Core Team, 2016).

## 3.3 Results

### 3.3.1 Characterization of the arthropod community

I recorded a total of 37,339 individuals representing 213 different arthropod morphospecies across the three different regions (Appendix F). The overall mean abundance was 69.8 (? 8.6), mean species richness was 14 (? 1.6) and mean species diversity was 3 (? 0.1) per core site for the sweep-net samples. Estimates of species diversity were similar between sampling methods; however, the estimated mean abundance (38.6 ? 3.7) and species richness (8.7) per core site was lower from the blow-vac samples.

Using the NMDS and Ward’s cluster analysis for the arthropod community collected with the blow-vac sampling method, I identified three significantly different assemblages (perMANOVA, R = 0.35, P = 0.001), representing the three study regions PH_1, PH_2 and PH_3 (Figure 3.3.1). An additional significant assemblage (PH_3b) was identified in the highland region when the analyses were applied to the sweep-net samples (Appendix G). In addition, significant spatial autocorrelation was observed among the core sites, as showed by a strong correlation between the dissimilarity matrix and a matrix of geographic distances between individual sampling plots (Mantel's R = 0.41, P = 0.001).

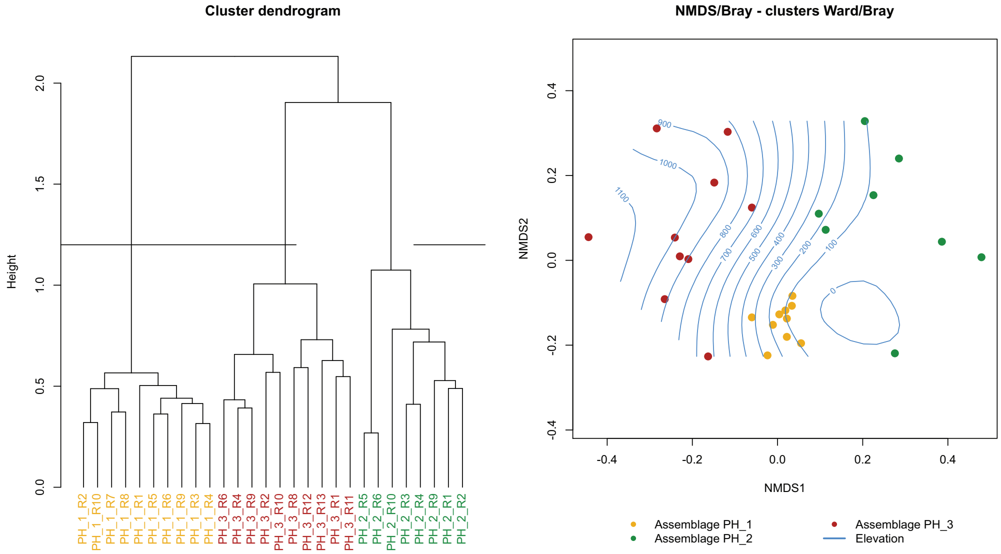


**Figure 3.3.1:** (a) Ward's hierarchical cluster analysis based on Bray-Curtis dissimilarity matrix using square-root transformed arthropod mean abundance data of 28 core sites (data shown for the blow-vac samples). The cluster analysis identified three distinct assemblages (distinguished by color), each associated with one region. Core sites are abbreviated using the following nomenclature: PH represents the region; R represents the core site (i.e. PH_1_R2: Core site number 2 located in the region PH_1). (b) Non-metric multidimensional scaling (NMDS) analysis of the Bray-Curtis dissimilarity matrix (data shown for the blow-vac samples). The distance between sites indicates similarity of the arthropod community-the closer, the more similar. The variable that best explained the assemblage structure (i.e. elevation) is shown as surface fitting.

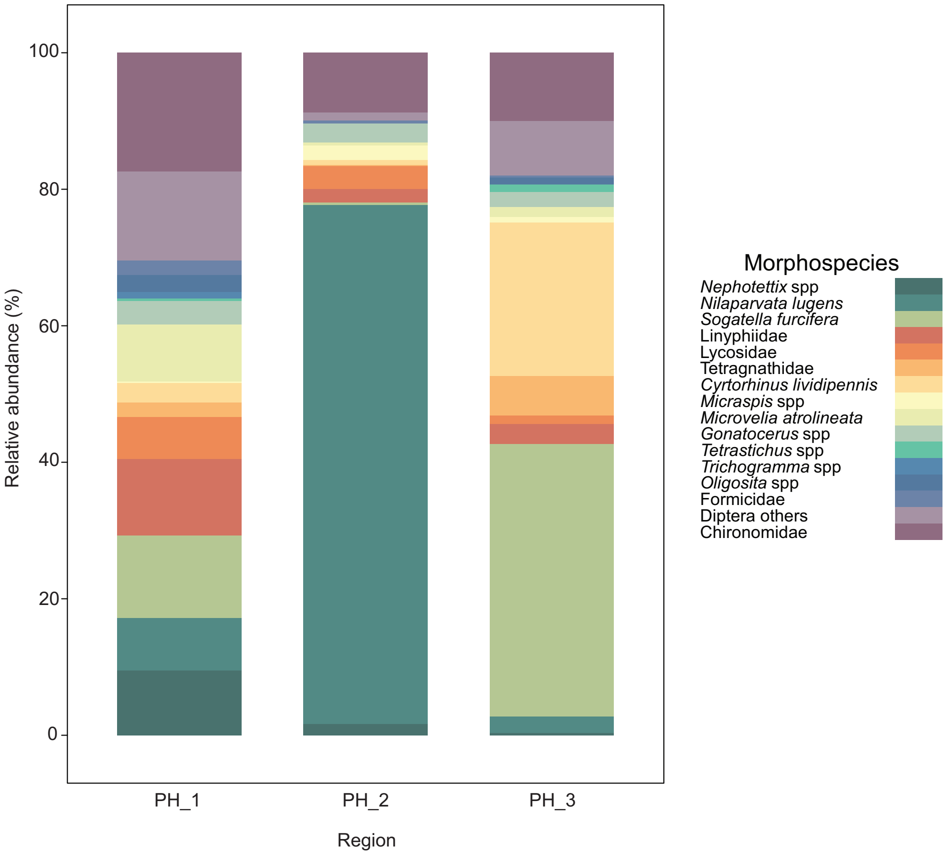


**Figure 3.3.2:** Relative abundances of 16 morphospecies (calculated by SIMPER analysis) that contributed the most to the similarities within each arthropod assemblage identified based on Bray-Curtis dissimilarity matrix (data shown for the blow-vac samples).

Located in the hilly Laguna Province, the assemblage PH_1 was the most homogeneous (average intra-group similarity: 58%) and its mean abundance (59.3 ? 2.8), species richness (17.3 ? 0.8) and species diversity (3.59 ? 0.05) were higher than the overall mean values across all regions. The arthropod communities located in PH_1 were characterized by a high abundance of detritivores/tourists such as chironomids, collembolans and other dipterans (~28% of the overall contribution; Fig. 3). The two main planthopper species, the brown planthopper, *Nilaparvata lugens*, and the whitebacked planthopper, *Sogatella furcifera*, were equally abundant. The predators were mostly represented by dwarf spiders (Linyphiidae) and wolf spiders (Lycosidae) (11% of the contribution). Based on their low intra-group similarity, both assemblages PH_2 and PH_3 (39% and 38%, respectively) were more heterogeneous than the assemblage PH_1. High abundances of lady beetles of the genus *Micraspis* and dwarf spiders were recorded in PH_2 (~22% contribution). While *N. lugens* contributed ~29% to the whole PH_2 assemblage, *S. furcifera* contributed less than 1% of the assemblage. On the other hand, in the PH_3 region, *S. furcifera* contributed ~19% to the assemblage, as opposed to *N. lugens* with less than 1%. The predatory mirid bug *Cyrtorhinus lividipennis* was collected in relatively high numbers at all sites in PH_3 (Figure 3.3.2).

*Sogatella furcifera* and chironomids were the most abundant arthropods collected in the sweep nets (~50% of the total abundance), while *N. lugens*, *S. furcifera* and chironomids were most abundant in the blow-vac samples (more than 30% of the total abundance). In addition, *N.lugens*, *S.furcifera*, chironomids, *Tetragnatha* spp. (Tetragnathadiae), *Microvelia atrolineata*, dwarf spiders, wolf spiders, and collembolans (Isotomidae) were the most widely distributed arthropods according to blow-vac samples (present at more than 80% of core sites).

*Nilaparvata lugens*, *Tetragnatha* spp., *Aranaea* spp. (Aranaeidae), chironomids, dipterans (other than chironomids) and *Micraspis* spp. were the most widely distributed species according to the sweep net samples (present in more than 80% of core sites). Sampling method had a significant effect on the relative abundances of most morphospecies (Figure 3.3.3). When comparing rarefied species richness for the populations sampled by blow-vac and sweep net, I found a statistical difference for the region PH_1 ($t = -3.635$, $P = 0.003$) and PH_3 ($t = -8.644$, $P < 0.001$) but no difference for PH_2 ($t = -1.745$, $P > 0.05$). Despite these differences in detected abundance and rarefied species richness, the results of the Mantel test showed a significant concordance between the blow-vac and sweep net sampling methods (Mantel's $R = 0.56$; $P = 0.001$), indicating a similarity of the overall species composition for both sampling methods.

### 3.3.2 Regional-scale effects and fine-scale landscape heterogeneity

The pairwise Pearson's correlation tests between temperature, precipitation and elevation revealed that all variables were highly collinear ($|r| > 0.7$, $P < 0.05$). I therefore used only elevation in further analyses as a proxy for overall regional-scale effects in the study regions (i.e. other climatic, environmental and broad-scale landscape conditions).

For both dissimilarity matrices based on the two sampling methods, I found no effect of fine-scale landscape heterogeneity on the assemblage structure ($P > 0.05$). In contrast, elevation explained 65% of variance in the blow-vac samples and 68% of variance in the sweep net samples ($P < 0.001$). An elevation gradient fitted on the NMDS plot is shown in Fig. 2b for the blow-vac community and in Appendix G2 for the sweep net community.

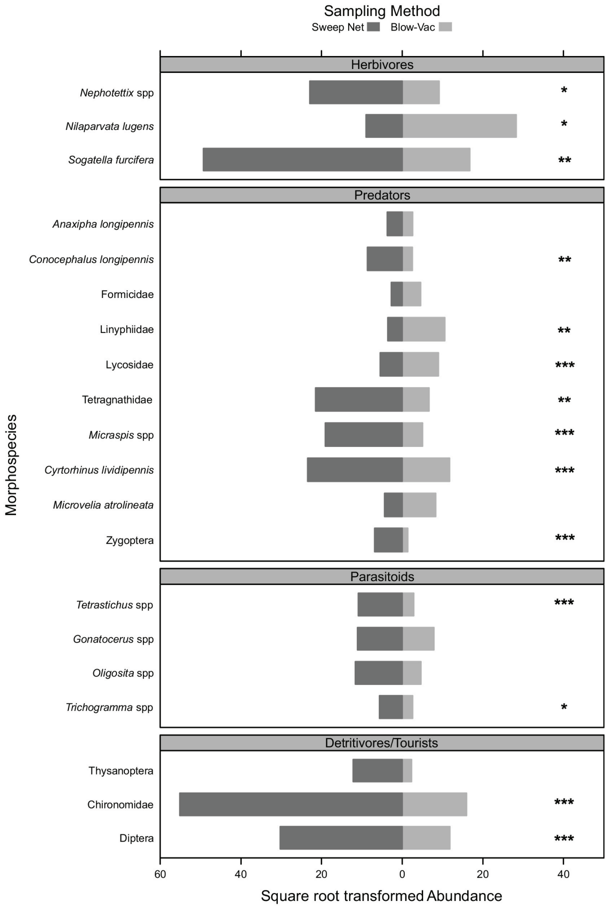


**Figure 3.3.3:** Comparison of the mean abundance of the 20 most common morphospecies collected with blow-vac and sweep net. The list of morphospecies is grouped into four functional groups (from top to bottom: Herbivores, Predators, Parasitoids, and Detritivores/Tourists). Significant differences between sampling methods are indicated by asterisks located next to the bar plots (* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$).

I also found no effect of fine-scale landscape heterogeneity on the total mean abundance, total species richness or total species diversity of the arthropod communities across all study sites. However, both the total mean abundance and total species richness of the communities were significantly negatively correlated with elevation ($F = 6.206$, $P < 0.05$ and $F = 9.175$, $P < 0.01$, respectively). When “region” was included as a random effect, it substituted the influence of elevation (the range of elevation differed greatly among regions, while being lower within each region) but provided the same results regarding the effects of fine-scale landscape heterogeneity. I found no effect of landscape heterogeneity at this scale on those morphospecies that contributed the most to each assemblage across all study sites.

However, I found multiple effects of elevation on the majority of morphospecies examined based on both the blow-vac and sweep net samples. Whereas most of the responses were negatively correlated with elevation, I found a positive correlation with elevation for the abundances of *S. furcifera* and *C. lividipennis* (F = 5.789, $P < 0.03$ and F = 4.988, $P < 0.02$ respectively) (Appendix H).

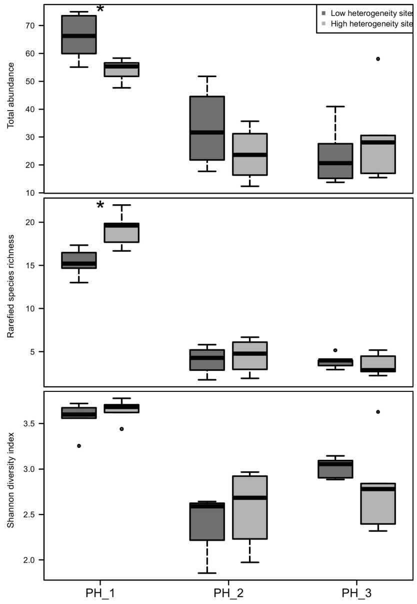


**Figure 3.3.4:** Box-plots of the total mean abundance, rarefied species richness and species diversity (Shannon diversity index) of arthropods in sites with high (dark grey) and low (light grey) levels of fine-scale landscape heterogeneity (data shown for the blow-vac samples). Boxes show the median, 25th and 75th percentiles, maximum and minimum observations. Significant differences ($P < 0.05$) are indicated by asterisks.

Comparing sites with high and low heterogeneity separately for each identified assemblage, I found significant differences only for abundance (t = 2.814, $P < 0.05$) and species richness (t = -3.225, $P < 0.02$) in PH_1 for samples collected with the blow-vac method (Figure 3.3.4). In all other cases no significant differences were observed. Similarly, the results showed a significant effect of fine-scale landscape heterogeneity on only a few functional groups. For the blow-vac method, I found significant differences between high and low heterogeneity sites only for the abundance of detritivores and predators in PH_1 (t = 3.149, $P < 0.05$ and t = 2.503, $P < 0.05$, respectively) (Figure 3.3.5), and the diversity of herbivores in PH_3 (t = 2.449, $P < 0.05$) (Appendix I). For the sweep net method, only the diversity of predators was affected by fine-scale landscape heterogeneity in PH_1 (t = -2.571, $P < 0.05$) (Appendix J). Furthermore, I found a significant effect of landscape heterogeneity at this scale only on two morphospecies (out of a total of 16) for the blow-vac community. In PH_1, the parasitoid *Oligosita* spp. was positively correlated with fine-scale landscape heterogeneity (t = 0.345, $P < 0.03$), while the aquatic predator *M. atrolineata* was negatively correlated with fine-scale landscape heterogeneity (W = 16, $P < 0.02$).

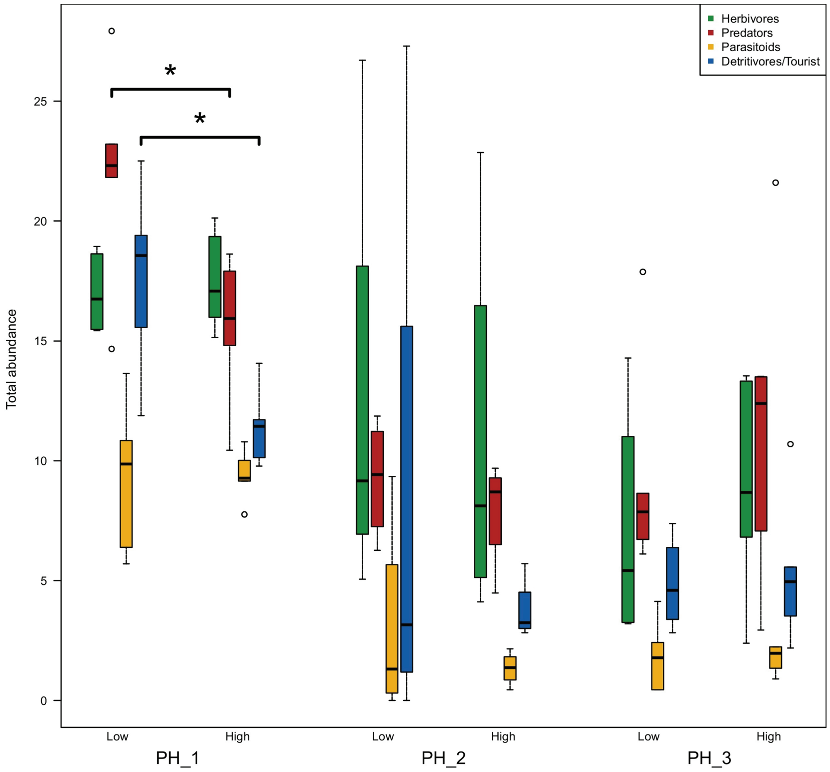


**Figure 3.3.5:** Box-plots of the total mean abundance of functional groups for low heterogeneity sites ("Low") and high heterogeneity sites ("High") across the three regions (data derived from the blow-vac). Boxes show the median, 25th and 75th percentiles, maximum and minimum observations. Significant differences ($P < 0.05$) between low and high heterogeneity habitats are indicated by asterisks above and between boxes.

## 3.4 Discussion

I recorded a total of 213 morphospecies across the three regions, which correspond well with the number of species documented by Barrion et al. (1994) (240 species) and by Heong et al. (1991) (212 species). In Barrion et al. (1994), Los Ba?os (Laguna Province) showed the highest diversity of arthropods (H' = 12.75), while Banaue (Ifugao Prov.) had a lower diversity (H' = 5.70) and Cabanatuan (a city located in Nueva Ecija Prov.) exhibited the lowest diversity (H' = 4.70). My results corroborate these findings, with PH_1 accounting for the highest species diversity, followed by PH_3 and PH_2. The results showing that assemblages PH_3 and PH_2 are the most dissimilar (75.9% based on NMDS) also corroborate with Schoenly et al. (1996) who indicated that rice communities in Banaue and Cabanatuan were the least taxonomically similar (25%).

Although most of the common arthropod species were present in all three regions, the community structure differed from one region to another, resulting in three distinct assemblages. The positive spatial autocorrelation identified among core sites further supports this observation, showing that samples collected from nearby locations were also compositionally more similar than samples from locations further apart. The assemblage located in PH_1 included a higher number of species, a higher relative abundance and higher species diversity of the rice arthropods than the assemblages in regions PH_2 and PH_3, in addition to being more homogeneous than the other two sites. The PH_1 assemblage had also a relatively high number of detritivores that can potentially boost the abundance of generalist predators, which use detritivores as an alternative prey and may contribute to the relatively high resilience of irrigated rice systems (Settle et al., 1996). The high number of detritivores likely supported high numbers of two generalist spider families, Linyphidae and Lycosidae, as found in the Laguna region. The most common species of these two families are the lycosid *Pardosa pseudoannulata* and the linyphiid *Atypena formosana* (Barrion and Litsinger, 1984; Kenmore et al., 1984; Sigsgaard, 2000), which are important regulators of rice herbivores (Reddy and Heong, 1991). This was also reflected in my results, as *N. lugens*, *S. furcifera* and the green leafhopper *Nephotettix* spp. were the three main rice herbivores found in similar numbers across the PH_1 assemblage.

The assemblage PH_2 of Nueva Ecija had the lowest abundance, species richness and diversity of arthropods and had higher evenness than the other two assemblages, as is expected in intensive monoculture systems. *Nilaparvata lugens* was the dominant herbivore in PH_2, contributing to nearly one third of the total assemblage, while *S. furcifera* and *Nephotettix* spp. were largely absent. However, low numbers of predators and parasitoids were observed, likely due to the low quality of potential habitats caused by the high proportion of rice monocultures in the region. In addition, *N. lugens* populations are known to increase drastically when main predators are removed (Kenmore et al., 1984). Modern rice varieties that are often accompanied by high levels of mechanization and chemical inputs (Burkhard et al., 2015) may also explain the disrupted assemblage structure in this region.

In the mountainous region of PH_3 Ifugao, *S. furcifera* was by far the most dominant herbivore species, representing nearly 20% of the total assemblage, whereas *N. lugens* contributed only 1%. The population of both herbivores in

PH_3 was likely regulated by a combination of various predators such as *P. pseudoannulata*, *A. formosana*, *Tetragnatha* spp. and *C. lividipennis* (Barrion and Litsinger, 1984). The predatory bug *C. lividipennis* is a major predator of delphacids that consumes planthopper eggs and nymphs (Sigsgaard, 2007) and can consume over seven *N. lugens* nymphs daily (Reyes and Gabriel, 1975). The high numbers of *C. lividipennis* in PH_3 can be explained by the overwhelming presence of *S. furcifera* nymphs collected in the samples (~70% of nymphs collected).

The results did not confirm the hypothesis that landscape heterogeneity within 100 m of sampling locations has a positive effect on the arthropod community. I found no effect of fine-scale landscape heterogeneity on assemblage structure and no differences in arthropod relative abundances, species richness or diversity between sites with a high and low level of landscape heterogeneity. Even when examining each identified assemblage separately, I found significant effects only in PH_1. Similarly, only one parasitoid and one predator out of the 16 morphospecies involved in the analyses, responded to landscape heterogeneity at this scale. In agreement with other studies of arthropods in agro-ecosystems (Altieri and Letourneau, 1982; Weibull et al., 2003; Wilby et al., 2006), the locations with higher landscape heterogeneity in PH_1 had higher species richness. However, the lower total abundance and lower abundance of both predators and detritivores in PH_1 suggest that the increased species richness observed in more heterogeneous sites may be compensated by lower abundances, especially in these two groups. For herbivores, I observed greater species diversity in the more heterogeneous sites of PH_3, but the predator group was neither more abundant nor diverse and therefore I cannot make any conclusion about the effect of landscape heterogeneity at this scale on natural pest control in the study regions.

These complex but largely inconclusive results regarding landscape heterogeneity may have several explanations. First, regional-scale effects, including effects of elevation, climatic conditions but potentially also landscape structure at a broader spatial scale than measured in this study, were more important than fine-scale landscape heterogeneity in explaining the composition of rice arthropod communities. Indeed, when I used elevation as a proxy for all regional-scale effects in the study regions, it explained the majority of variance (>60%) in the assemblage structure based on the dissimilarity matrices (Fig. 2b, Appendix G2). The differences in the variability of arthropod composition among study regions can be further illustrated by the differences in variability of elevation and climate conditions in those regions (Appendix E). Moreover, not only did I find that total arthropod abundances decreased with increasing elevation, similarly as in Schoenly et al. (1996), but I also found that the total rarefied species richness decreased with increasing elevation. In addition, the results are in agreements with the conclusions of Hodkinson (2005); who showed that responses of species abundance to elevation are known to vary with taxa and location. While the abundance of most of the morphospecies such as *N. lugens*, *Nephotettix* spp., lycosids, linyphiids and chironomids decreased with elevation, two species, *S. furcifera* and *C. lividipennis*, found in high numbers in PH_3 were positively affected by elevation. These findings are also supported by a previous study showing that elevation is a limiting factor for the fitness of *N. lugens* (Settele, 1992).

Second, the investigated arthropod communities were potentially co-affected by other factors that are unique to each study region but were not accounted for in the design of this analysis. The study was conducted in a real agricultural setting in which land-use intensity, cropping synchrony, pesticide inputs or other land management factors were not controlled. Although I assume that these factors did not vary systematically across the sites with high and low levels of fine-scale landscape heterogeneity, their specific character in each study region may have contributed to the high variability in my dataset and to the clear differences in the assemblage structure among study regions. In addition, the variability of elevation and climate was high among regions but low within regions. This further suggests that the effects of other factors specific to the regions, such as broad-scale landscape structure or the intensity of land use, cannot be fully disentangled from the overall regional effects without specifically controlling for them in the analysis.

Third, the scale and the binary distinction between sites with high and low heterogeneity may be insufficient to detect landscape effect on the rice arthropod fauna. While the differentiation of the two landscape heterogeneity levels around sampled fields was consistent for all regions, the broad-scale landscape structure among the three regions varies considerably (Burkhard et al., 2015). For example, the overall region PH_1 in Laguna is characterized by rice production landscapes with close proximity to numerous agricultural fields, gardens, ponds and semi-natural habitats. In contrast, rice fields in the region PH_2 of Nueva Ecija occupy over 95% of the land area, with each field being separated only by a network of terrestrial bunds combined with a low diversity of other habitats. Although the scale of a few hundred meters was previously found sufficient to show landscape effects in rice agro-ecosystems (Wilby et al., 2006), many rice invertebrates are known to migrate over considerably larger distances (e.g. Reynolds et al., 1999). In addition, the potential effects of a broad-scale landscape structure were likely confounded with the influence of environmental conditions that I accounted for in the analysis at the regional scale. Therefore, I suggest that future research should focus on a more detailed quantification of landscape heterogeneity (e.g. using metrics of landscape composition, configuration and intensity of use (Seppelt et al., 2016)) and examine its effect at multiple spatial scales that match the migratory abilities of the investigated rice arthropods.

I used two different sampling methods to assess the arthropod communities in the rice fields. The sweep net method was more efficient to sample leaf canopy arthropods such as chironomids, other dipterans, parasitoids and long-jawed orb weavers (Tetragnathidae). Samples taken with the sweep net were collected typically at the top of the rice canopy, since the lower surface of the plant was unreachable without damaging the plant. Arthropods that dwell low on the plant or on the water surface, i.e. *N. lugens*, dwarf spiders or lycosids, were caught in significantly greater numbers by the blow-vac. The combination of multiple sampling methods in rice fields is thus generally advised to properly assess arthropod biodiversity (Doxon et al., 2011). However, in this study, while differences in abundance of specific taxa were observed between sampling methods, both methods provided samples with similar species composition. This suggests that, in cases of limited time or resources, the use of only one method may be acceptable when the focus is on community composition rather than on species abundance.

## 3.5 Conclusion

I characterized and compared rice arthropod communities from three important rice production regions in the Philippines that differed in environmental conditions as well as in their level of landscape heterogeneity. First, the rice agro-ecosystems in each study region had relatively distinct arthropod assemblages, likely reflecting specific environmental conditions or land management factors in the regions. Second, the effect of fine-scale landscape heterogeneity was identified only in one region and only for two functional groups and two morphospecies, suggesting that regional-scale effects rather than fine-scale landscape heterogeneity explain the composition of rice arthropod communities in the study area. To further disentangle the complex effects of broad-scale environmental drivers versus fine-scale landscape context on arthropod communities and the biocontrol services, future studies of rice agro-ecosystems should apply more complex procedures of quantifying the spatial structures of rice fields and the surrounding habitats and examine their effect at multiple spatial scales.

# Chapter 4

# Landscape composition, configuration, and trophic interactions shape arthropod communities in rice agro-ecosystems

## 4.1 Introduction

The importance of landscape heterogeneity in agricultural landscapes for the maintenance of regulatory ecosystem functions, including herbivore regulation, has often been discussed in the scientific literature (Way and Heong, 1994; Altieri, 1999; Tscharntke et al., 2005). Several authors suggest that monocultures are associated with declining regulatory services and consequent pest outbreaks (Altieri, 1999). Because agro-ecosystems depend on a variety of ecosystem services, notably biological pest control (Bianchi et al., 2006; Losey and Vaughan, 2006), there has been an increased focus in recent years on methods such as "conservation biological control", to maximize agricultural productivity (Bengtsson et al., 2005; Bianchi et al., 2006; Letourneau and Bothwell, 2008). Such approaches aim to enhance natural enemy populations by manipulating the habitat surrounding crops to provide alternative food sources, such as prey, pollen and nectar, and a refuge from agricultural disturbances and thereby enhance the abundance and functional efficiency of natural enemies (Landis et al., 2000; Gurr et al., 2004).

The biodiversity present in rice landscapes in tropical Asia is often higher than in many natural ecosystems, as many of the species inhabiting rice fields are specialized, open grassland species (Schoenly et al., 1998; Dominik et al., 2017). Nevertheless, the intensification of rice cropping, in combination with the (over)use of insecticides, has led to disruptions in the interactions between herbivores and their natural enemies, resulting in often severe pest outbreaks (Heinrichs et al., 1982; Heinrichs and Mochida, 1984; Schoenly et al., 1996; Heong and Schoenly, 1998). Several studies have shown that unsprayed rice fields in less intensive farming systems have fewer pest problems and display little to no crop losses (Kenmore et al., 1984; Way and Heong, 1994; Horgan et al., 2017). Settele et al. (2008) have called for a switch to conservation biological control (also called ecological engineering; see Gurr et al., 2004) in rice agro-ecosystems. However, to date only a few studies have focused on the potential benefits of landscape heterogeneity or habitat manipulation for the natural enemies of rice pests (Lin et al., 2011; Yao et al., 2012; Gurr et al., 2016; Horgan et al., 2017).

Two aspects determine landscape heterogeneity: (i) landscape composition (diversity of landscape features and habitat types) and (ii) landscape configuration (number, size and connectivity of habitat patches) (Seppelt et al., 2016). The composition of rice landscapes in tropical Asia is characterized by a mosaic of different habitats that include the rice crop itself, other crops, fallow fields and natural vegetation. The diversity of habitat patches, neighboring the rice fields, may influence pests, natural enemies, and other biological components of the agroecosystem by modifying the extent of host and prey resources or the quality of microclimatic conditions (Pickett and Bugg, 1998; Landis et al., 2000). Since Asian rice farmers typically own small areas of land (often $< 2$ ha), the configuration of rice habitats is characterized by a relatively large number of small-sized habitat patches with varying degrees of connectivity. Habitat fragmentation is known to negatively affect natural enemies in temperate agricultural landscapes (i.e. parasitoids: Kruess and Tscharntke, 1994; Thies and Tscharntke, 1999; Tscharntke and Kruess, 1999; predators: Tscharntke and Kruess, 1999). However, rice fields are connected through an extensive network of bunds (levee of terrestrial area surrounding the fields), typically with sparse semi-natural vegetation that can potentially offer alternative food resources or refugia to natural enemies (Way and Heong, 1994). The presence of bunds likely facilitates the ability of rice arthropods to move through the rice agroecosystem. For example, egg parasitoids of the genera *Anagrus* and *Oligosita* that cause high mortality of pest planthoppers such as *N. lugens* and *S. furcifera*, occur in wild grasses on rice bunds (Yu et al., 1996). Furthermore, the spider *P. pseudoannulata*, which commonly inhabits bund vegetation, is known to be an early colonizer of newly established rice crops (Sigsgaard, 2000). However, the effects of rice bunds and their functional connectivity on the community composition of rice arthropods are still poorly understood at landscape scales.

In the tropical rice agro-ecosystems in the Philippines, regional-scale effects (e.g. the effects of elevation as a proxy for climate and other landscape factors) rather than fine-scale landscape heterogeneity explain much of the structure of the arthropod community (Dominik et al., 2017). However, the composition and spatial arrangement of habitat patches can also affect community structure at certain spatial scales (Pickett and Cadenasso, 1995; Roland and Taylor, 1997). Such scale effects are primarily driven by species mobility and thus vary across species (Ricketts, 2001; Horner-Devine et al., 2003; Jackson and Fahrig, 2012).

There is growing evidence that predators and parasitoids are key to regulating herbivore densities in rice agro-ecosystems (Kenmore et al., 1984; Schoenly et al., 1996; Settle et al., 1996). Due to high arthropod diversity in many agro-ecosystems and particularly in tropical rice fields, taxa are often categorized into functional groups to condense information on the huge diversity and provide a research approach to study both food web complexity and community dynamics (Heong et al., 1991; Heong et al., 1992; Settle et al., 1996). Functional groups are a useful descriptor for linking population and ecosystem processes, and for defining the functional differences between herbivores (pests when at high density), natural enemies (predators and parasitoids) and detritivores/tourists (i.e. non-predatory species that have no direct association with the rice plant but which may be attracted to surrounding habitats; Moran and Southwood, 1982). However, less is known about the way in which trophic interactions have shaped arthropod communities at broader scales, and within the context of landscape heterogeneity. Wiens (2011) suggested that trophic interactions rarely play a role at the landscape scale, or that there are simply too few studies to fully explore the issue.

An increasing number of studies support an idea that the efficiency of natural enemies in regulating herbivores can be enhanced by increasing the structural and compositional diversity of rice-associated habitat (Gurr et al., 2016; Horgan et al., 2016; Horgan et al., 2017). Most of this research has been conducted at field and plot scales without regard to the influence of natural vegetation outside and often distant from the experimental plots or fields. This could be an important oversight leading to variability in the success of interventions such as “ecological engineering” that manage rice bunds to enhance natural enemy habitat (e.g., see differences between results from Yu et al., 1996, Yao et al., 2012 and Gurr et al., 2016 and those from Horgan et al., 2017 and Sann et al., 2018). Success might depend on the availability of suitable natural vegetation at scales hitherto omitted from research protocols or on the connectivity and form of rice bunds. Therefore, in this study, I compile a unique dataset on rice arthropods sampled from 28 field plots in tropical rice agro-ecosystems in the Philippines. For the first time, I quantify the heterogeneity of managed rice landscapes surrounding each sampling site based on high-resolution satellite imagery using four independent metrics of landscape composition and configuration. To my knowledge, this is the first study to separate the influences of associated habitat, rice bunds and the trophic composition of rice-associated arthropods on the biocontrol potential of rice landscape. Understanding the influence of such factors in rice is particularly valuable because of architectural restrictions in the design of rice landscapes that require scheduled flooding and draining. I examine the combined effects of landscape heterogeneity and trophic interactions on arthropod communities, particularly the natural enemies, and identify the spatial scales at which these effects are most pronounced. Specifically, I test the following hypotheses:

1) Landscape diversity has positive effects on the abundance and species richness of natural enemies;
2) The configuration of rice habitats (size of habitat patches and connectivity of rice bunds) has positive effects on the abundance and species richness of natural enemies; and
3) The abundance of natural enemies responds to the abundance of prey.

## 4.2 Materials and methods

### 4.2.1 Study regions

The study was conducted within the project LEGATO (Settele et al., 2015) across three 15 x 15 km regions along an elevation gradient on the island of Luzon in the Philippines as described in 2.1.1. The three regions were: (i) a rice landscape in the hilly lowlands of Laguna Province in southern Luzon (PH_1); (ii) an intensively cultivated rice landscape in Nueva Ecija Province (PH_2) situated in central Luzon ; and (iii) a traditional terraced rice system in the mountainous Ifugao Province located in the north of Luzon (for details, see Klotzbücher et al., 2015; Dominik et al., 2017; Langerwisch et al., 2017). Within each region, 10 core sites were selected, resulting in a total of 28 core sites (sampling could not be performed at two core sites in PH_2 because vegetables were planted instead of rice at the time of sampling). The average distance between the nearest cores sites was ~ 369 m.

### 4.2.2 Arthropod sampling

The arthropod communities present in the rice fields were sampled during the dry season of 2013 in PH_1 and PH_2 (double cropping is practiced in these regions; however, I only sampled during the wet season) and during the single cropping season of 2014 in PH_3 (which largely corresponded with the Luzon dry season). All samples were collected at the maximum tillering stage of the rice plant (50 days after transplanting) to ensure consistency of sampling; this stage is generally associated with a maximum abundance of arthropods (Heong, Aquino and Barrion 1991; Wilby et al., 2006). Since the composition of arthropod communities can change with the development of the rice crop and between cropping seasons (wet and dry seasons: Heong et al., 1991), the analyses focused on the data obtained during the dry season only (January to June).

Arthropods were collected using a modified leaf blower-vacuum (as described by Arida and Heong, 1992) (see 2.3.1). Collected arthropods were preserved in 70% ethanol, sorted and identified to species level (or to morphospecies where specimens could not be adequately identified to species level) using a binocular microscope and the taxonomic keys of Barrion and Litsinger (1994). Morphological similarity at the pre-adult stages and quality of the samples limited the identification of arachnids, dipterans and collembolans to family level. Additionally, arthropods were grouped into functional groups as follows: (i) herbivores; (ii) predators; (iii) parasitoids; and (iv) detritivores and tourists.

### 4.2.3 Mapping and landscape metrics

All landscape features were identified and mapped within a 300-m radius around each sampling site using heads-up digitizing in a geographic information system (ArcGIS 10.3, ESRI) based on high-resolution SPOT-5 DIMAP images (2.5 m). In addition, I collected ground-truth data in June 2014 to verify the photo-interpretation using Collector for ArcGIS (version 9.3, ESRI). I randomly attributed 10 ground-truth locations within each 300 m buffer, verified the land cover in the field and if necessary corrected the digitized maps. Land cover features were classified at a consistent scale of 1:1000 into eight final categories: rice fields, woodlands, grasslands, artificial areas, plantations, rice bunds, hydrographic network, and ponds (see Figure 2.2.1).

To quantify landscape heterogeneity around sampling sites, I calculated four independent metrics of landscape composition and configuration within three buffer distances (100, 200 and 300 m radii) using Fragstats 3.3 (McGarigal and Marks, 1995). As a measure of compositional landscape heterogeneity, I used the Shannon"s diversity index (SHDI) calculated at the landscape level with all eight land cover categories. Three metrics of configurational landscape heterogeneity focused on the rice habitat and quantified the connectivity, number/size and shape complexity of rice habitat patches. The rice agroecosystem is usually composed of several rice fields (typically 1-3 ha in size) interconnected by a network of terrestrial levees (bunds). Therefore, we calculated the patch cohesion index (COH) to quantify the structural connectivity of rice bunds and the number of patches (NP) to represent the degree of rice habitat fragmentation (higher numbers representing more fragmented habitat with smaller mean patch size). Finally, I measured the shape complexity of each rice field using the fractal dimension index (FRAC) because the shape of habitat patches may affect the arthropod communities via edge effects, e.g. influencing host finding due to the way that plant odors are emitted from habitat patches (Stanton, 1983). These landscape metrics were selected because (i) they were not correlated with each other, (ii) they allowed easy interpretation and (iii) they described unique characteristics of landscape heterogeneity (diversity, connectivity, size and shape).

### 4.2.4 Statistical analyses

The responses of rice-arthropod communities to landscape heterogeneity were analyzed using linear mixed-effect models for each response variable and each spatial scale (100, 200 and 300 m). The response variables were (i) the species richness within functional groups, (ii) the abundance within functional groups, and (iii) the abundance of the most common species (present in at least 20% of the total samples and representing at least 10% of all collected organisms in any sample). The abundance of all arthropods was log-transformed prior to analyses to meet the assumptions of normality (Pinheiro et al., 2015). Since each region has relatively distinct arthropod assemblages and rice management practices (Dominik et al., 2017), subsamples nested within "region" (PH_1, PH_2 and PH_3) were assigned as a random effect. The four metrics of compositional and configurational landscape heterogeneity (i.e. SHDI, NP, COHESION and FRAC) were assigned as fixed effects. Although the main focus of this study was to test the effects of landscape heterogeneity, I included elevation as another predictor because this variable, being a proxy for regional-scale climatic conditions and land-use intensity, has been previously shown to determine the arthropod community composition in the study areas (Dominik et al., 2017). Climate data were obtained from the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global Digital Elevation Model (GDEM) V2 at a 30-m resolution (https://lpdaac.usgs.gov/). A stepwise regression procedure was used together with testing all variable combinations to determine the best-fitting model based on the lowest AICc score. The procedure was repeated separately for each response variable and spatial scale.

To account for trophic interactions, additional fixed effects were added to the full models when testing the responses of abundance of individual functional groups. As predator-prey interactions between natural enemies and other functional groups are expected, especially herbivores, the abundance of both predators and parasitoids were added to the model for herbivores and, similarly, the abundance of detritivores/tourists and herbivores were added to the model for predators. Detritivores act as a primary source of food during the early stages of the rice plant for many generalist predators (Settele, 1992; Settle et al., 1996; Gurr et al., 2016). However, interactions between parasitoids and other groups (except for herbivores) have not been documented, thus only the abundance of herbivores was added to the model for parasitoids. Finally, the abundance of predators was included when testing responses in the abundance of detritivores/tourists. Again, the best-fitting models were determined across all spatial scales by selecting the models with the minimal AICc scores.

All statistical analyses were conducted using the *lme* function in the *nlme* package (Pinheiro et al., 2014) in R version 3.1.1 (R Development Core Team 2016).

## 4.3 Results

In total, I collected 8547 individuals and identified 113 different arthropod morphospecies across the three study regions. Herbivores accounted for 36.8% of the total arthropods collected and were dominated by the Whitebacked Planthopper (*Sogatella furcifera*), the Brown Planthopper (*Nilaparvata lugens*), and Green Leafhoppers (*Nephottetix* spp). Predators contributed 26.9% of the total abundance and were mostly represented by dwarf spiders (Linyphiidae), wolf spiders (Lycosidae), long-jawed orb weavers (Tetragnathidae), lady beetles of the genus *Micraspis*, and the mirid bug *Cyrtorhinus lividipennis*. The detritivores/tourists group represented 29.6% of the total arthropod abundance and was mainly composed of chironomids and collembollans (Isomotidae, Sminthuridae, and Entomidae). Finally, parasitoids accounted for 6.7% of the total abundance and were mainly represented by *Gonatocerus* spp and *Oligosita* spp.

### 4.3.1 Landscape heterogeneity

All best models included the combined effects of compositional or configurational landscape heterogeneity and trophic interactions. However, each functional group and more common species responded differently to landscape heterogeneity (Figure 4.3.1). Elevation explained only the abundance of parasitoids (t = 2.766, $P$ = 0.011) and the predator *C. lividipennis* (t = 3.278, $P$ = 0.003).

The abundance of herbivores, including the more common species, declined with increasing landscape diversity (SHDI) (t = -3.383, $P$ = 0.003) (Figure 4.3.1a). The scale at which herbivores species responded to landscape diversity varied from one species to the next but the best model for herbivores was based on habitat characteristics defined at 300 m (Table 4.3.1). Additionally, landscape diversity was negatively correlated with the abundance of Sminthuridae (t = -2.769, $P$ =

| | | Scale | Elevation<br>DEM | | Landscape diversity<br>SHDI | | Connectivity<br>COH | | Fragmentation<br>NP | | Shape<br>FRAC | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | *t* | *P* | *t* | *P* | *t* | *P* | *t* | *P* | *t* | *P* |
| **Abundance** | | | | | | | | | | | | |
| | **all Herbivores** | 300m | | | **-3.383** | **0.003** | | | **-4.002** | **0.001** | | |
| | ***Sogatella furcifera*** | 300m | | | **-3.941** | **0.001** | | | **-3.009** | **0.006** | | |
| | ***Nilaparvata lugens*** | NA | | | | | | | | | | |
| | ***Nephotettix spp*** | 200m | | | **-3.808** | **0.001** | | | | | | |
| | **all Predators** | NA | | | | | | | | | | |
| | ***Cyrtorhinus lividipennis*** | NA | **3.278** | **0.003** | | | | | | | | |
| | **Linyphiidae** | 300m | | | | | | | | | **-2.356** | **0.016** |
| | **Lycosidae** | NA | | | | | | | | | | |
| | **Tetragnathidae** | 300m | | | | | **3.596** | **0.002** | **-4.394** | **0** | | |
| | ***Micraspis spp*** | 300m | | | | | | | **3.299** | **0.003** | **-2.268** | **0.033** |
| | **all Parasitoids** | 300m | **2.766** | **0.011** | | | **5.753** | **0** | **-3.93** | **0.001** | | |
| | ***Gonatocerus spp*** | NA | | | | | **2.458** | **0.022** | | | | |
| | ***Oligosita spp*** | 300m | | | | | **4.628** | **0** | **-4.575** | **0** | **2.688** | **0.033** |
| | **all Detritivores** | 200m | | | | | **2.762** | **0.011** | | | | |
| | **Chironomidae** | 200m | | | | | **2.36** | **0.027** | | | **-2.158** | **0.042** |
| | **Isomotidae** | NA | | | | | | | | | | |
| | **Sminthuridae** | 100m | | | **-2.769** | **0.01** | | | | | | |
| | **Entomidae** | NA | | | | | | | | | | |
| **Richness** | | | | | | | | | | | | |
| | **all Herbivores** | 300m | | | | | | | **-2.069** | **0.049** | | |
| | **all Predators** | 100m | | | | | **2.42** | **0.023** | | | | |
| | **all Parasitoids** | 300m | | | | | **3.528** | **0.002** | **-2.381** | **0.026** | | |
| | **all Detritivores** | NA | | | | | | | | | | |

**Table 4.3.1:** Results of the best-fitting linear mixed-effect models (based on the lowest AICc): the effects of elevation (DEM). landscape diversity (SHDI). structural connectivity (COH). fragmentation of the rice habitat (NP). and shape complexity of the rice patches (FRAC) on the abundance (log-transformed) and species richness of functional groups and more common species. The scale at which the effect of landscape heterogeneity was most pronounced (landscape metric entered the best model) is shown as: 100m. 200m. 300m. and NA when the scale is undetermined.

0.010), a family of detritivores. I found no effect of landscape diversity on the abundance or species richness of predators and parasitoids.

In agreement with my second hypothesis, the structural connectivity of the rice bunds (COH) increased the abundance and species richness of most natural enemies, particularly the parasitoids. The abundance (t = 5.753, $P = 0.000$) and number of parasitoid species (t = 3.528, $P = 0.002$) were strongly correlated with the structural connectivity of rice bunds at the scale of 300 m (Figure 4.3.1b). The connectivity of rice bunds also best explained the abundance of *Oligosita* spp (t = 4.628, $P < 0.001$) and *Gonatocerus* spp (t = 2.458, $P = 0.022$). The structural connectivity of rice bunds was also the only landscape metric, which explained the species richness of predators. The abundance of long-jawed orb weaver spiders (Tetragnathidae) was also positively correlated with the structural connectivity of rice bunds (t = 3.596, $P < 0.002$). The same effect was found for the abundance of detritivores/tourists (t = 2.762, $P = 0.011$) and chironomids (t = 2.360, $P = 0.027$) (Figure 4.3.1b).

The fragmentation of the rice habitat to smaller patches, represented by the number of rice patches (NP), negatively influenced arthropod communities. The abundance of both herbivores (t = -4.002, $P < 0.001$) and parasitoids (t = -3.930, $P < 0.001$) declined with increasing number of rice patches, measured at 300 m radii (Figure 4.3.1c). Similarly, the same pattern emerged with the number of parasitoid species (t = -2.381, $P = 0.026$). At the species level, the more common species of all groups were negatively correlated with the number of rice patches (Table 1). Surprisingly, only the abundance of the predatory Coccinellidae *Micraspis* spp increased significantly with the number of rice patches (t = 3.299, $P < 0.003$).

The shape complexity of the rice fields (FRAC) did not influence the total abundance or species richness of the functional groups. However, the shape complexity of the rice fields negatively influenced the abundance of some common species such as spiders from the Linyphiidae family (t = -2.356, $P = 0.016$), ladybugs of the genus *Micraspis* (t = -2.268, $P = 0.033$), and chironomids (t = -2.158, $P = 0.042$). In contrast, the parasitoids *Oligosita* spp. responded positively to the shape complexity of the rice fields (t = 2.688, $P = 0.013$).

The scale at which the arthropods responded to landscape heterogeneity varied between functional groups and between species. By comparing the AICs score among the models, the largest scale was constantly favored when arthropods responded to two or more scales. The detritivores/tourists group responded to landscape heterogeneity at a smaller scale than the other groups (200 m and below). Highly mobile arthropods such as parasitoids were typically influenced by landscape heterogeneity at the largest scale (300 m).

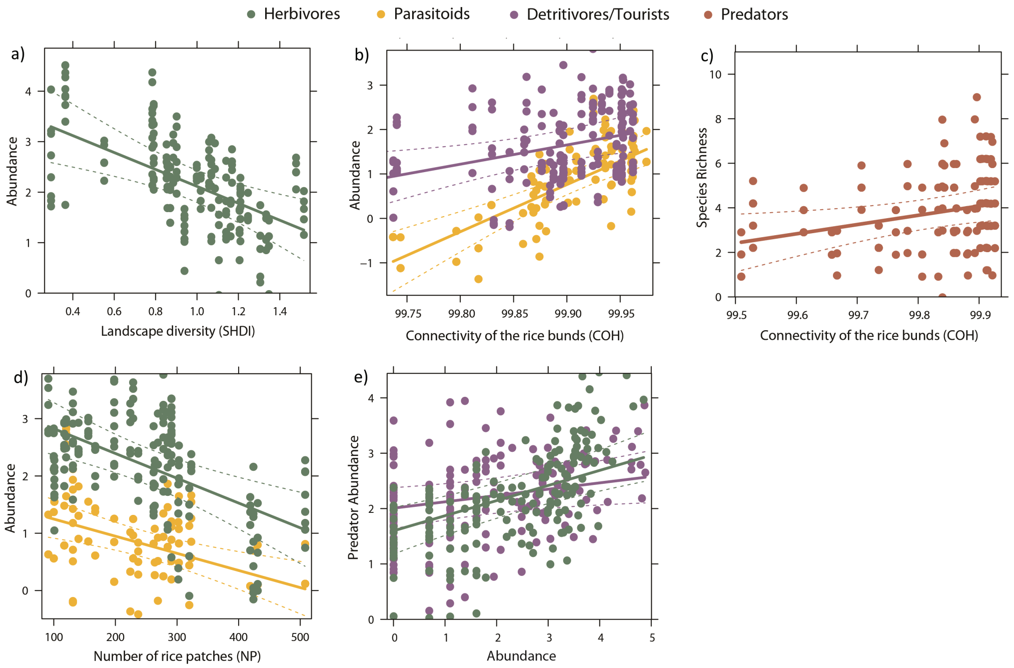


**Figure 4.3.1:** Linear mixed effects models representing relationships between (a) landscape diversity (SHDI) and abundance of herbivores, (b) structural connectivity of the rice bunds (COH) and abundance of detritivores/tourists and parasitoids, (c) structural connectivity of the rice bunds (COH) and species richness of predators, (d) number of rice patches (NP) and abundance of both herbivores and parasitoids, and (e) trophic interactions between predators, herbivores, and detritivores/tourists. All abundance data were log-transformed.

### 4.3.2 Trophic interactions

In addition to the effects of landscape heterogeneity, I found significant trophic interactions between herbivores, predators and detritivores/tourists (Table 4.3.2). The abundance of predators was highly dependent on the abundance of herbivores (t = 3.841, $P < 0.001$). While no effects of landscape composition were found on the abundance of predators, both the abundance of herbivores (t = 4.587, $P < 0.001$) and detritivores (t = 2.037, $P = 0.043$) explained the abundance of predators (Figure 4.3.1d). I found no effects of trophic interaction on the abundance of parasitoids.

| | | **Trophic interactions** | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Herbivores | | Predators | | Parasitoids | | Detritivores | |
| | | *t* | *P* | *t* | *P* | *t* | *P* | *t* | *P* |
| **Abundance** | | | | | | | | | |
| | all Herbivores | | | 3.841 | 0 | | | | |
| | all Predators | 4.587 | 0 | | | | | 2.037 | 0.043 |
| | all Parasitoids | | | | | | | | |
| | all Detritivores | | | 2.379 | 0.019 | | | 2.037 | 0.043 |

**Table 4.3.2:** Results of linear mixed model analyses on the effects of trophic interactions (abundance) between herbivores, predators, parasitoids, and detritivores.

## 4.4 Discussion

The responses of arthropod communities to the effects of landscape heterogeneity and trophic interactions greatly differed from one functional group to the next. Although landscape diversity did reduce the abundance of herbivores, it had no effects on the population of natural enemies. The abundance of parasitoids was better explained by the structural connectivity of the rice bunds, rather than by trophic interactions. In contrast, the abundance of predators was solely explained by the availability of prey, showing no significant response to any form of landscape heterogeneity.

### 4.4.1 Landscape heterogeneity

My analyses did not support my first hypothesis that landscape diversity has a positive effect on the abundance and species richness of the natural enemies of rice herbivores. However, I found that landscape diversity reduced the abundance of the herbivore group as well as the abundance of two common herbivore genera *Sogatella* and *Nephottetix*. This is potentially explained by the fact that increasing landscape diversity reduces the amount of crop habitat, i.e. the primary area where herbivores thrive. While heterogeneous landscapes with a diversity of habitat types generally increase biodiversity and ecosystem services in agricultural systems, natural non-crop habitats do not always have significant effects on pest control (Tscharntke et al., 2016; Sann et al., 2018). The absence of landscape diversity effects on natural enemy populations may be due to the fact that, even for natural enemies, crops represent more important food and habitat resource than other surrounding habitat types. In the study regions, asynchronous cropping creates a mosaic of cultivated and temporarily unused fields that provide a continuous supply of resources for predators and parasitoids over space and time, helping them to avoid spatial and temporal bottlenecks (Schoenly et al., 2010). In contrast, synchronous cropping could promote more frequent and intense pest outbreaks of green leafhopper (*Nephottetix* spp.) and brown planthopper (*N.lugens*) populations (Widiarta et al., 1990; Sawada et al., 1992). Wilby et al. (2006) showed that local landscape heterogeneity (measured as different crop, crop stage and habitat types) could influence rice-arthropod communities at different stages of the rice plant.

My observation of strong positive effects of the structural connectivity of bunds on the abundance and species richness of parasitoids is in agreement with Yu et al. (1996), who demonstrated that the egg parasitoids of *Anagrus* spp. and *Oligosita* spp. consumed eggs of non-pest planthoppers in wild grasses on rice bunds during fallow periods when fields were without a rice crop. In this study, the structural connectivity also positively influenced the detritivore/tourist populations. In general, field margins have greater arthropod abundance and diversity than the agricultural fields (Denys and Tscharntke, 2002; Botero-Garcès and Isaacs, 2004) and can provide potential refuge and food resources for flower-visiting, non-pest insects and predatory arthropods (Lagerlöf and Wallin, 1993). The suitability of these field margins as habitat for natural enemies can also depend on the width of the margin and the way margin vegetation is managed. With regard to pest management in rice, new ideas such as ecological engineering aim to manipulate the habitat on rice bunds to enhance biological control (Gurr et al., 2004; Horgan et al., 2016). By increasing the diversity and density of nectar flowering plants along the rice bunds, the fecundity and longevity of many predators and parasitoids potentially increase because they find alternative food resources such as pollen and nectar (Landis et al., 2000; Pickett and Bugg, 1998). The application of ecological engineering at the farm scale has been associated with higher abundances of predators and parasitoids across sites in China, Thailand and Vietnam (Gurr et al., 2016). However, several authors have also indicated that some plants that are commonly used in flowering strips fail to promote natural enemy populations at the field scale (Lin et al., 2011; Yao et al., 2012; Horgan et al., 2017). Additionally, parasitoids were found to be more abundant in rice habitats than in agroforests (Sann et al., 2018). My results indicate that discrepancies between the results of previous studies could be related to factors such as bund connectivity and field size. I found that the effects of connectivity were most pronounced when measured at the scale of 200-300 m. This suggests that the structural connectivity of bunds surrounding rice fields can potentially contribute to the functional connectivity of highly mobile arthropods such as parasitoids, and that interventions to increase the connectivity of field margins should focus on larger scales, e.g. at least several hundreds of meters.

The arthropod communities in this study strongly responded to the number of rice patches within the defined buffers around sampling sites. Patch area and fragmentation have often been associated with the richness of arthropods (Kruess and Tscharntke, 1994; Steffen-Dewenter et al., 2002). Habitat fragmentation can lead to disruption of the food chain and trophic structure, with predators being generally more vulnerable to fragmentation than their prey. This study shows that the fragmentation of rice fields negatively influences the richness and abundance of parasitoids but also of herbivores. Specialists such as rice herbivores (e.g., *N.lugens* and *S.furcifera*) are more likely to show a positive density-area relationship in their feeding habitat type than are habitat generalists (i.e., Hambäck et al., 2007). Additionally, parasitoids are often less effective in searching for food resources when in fragmented landscapes (Kruess and Tscharntke, 1994; Tscharntke and Brandl, 2004). However, I did not find the expected negative correlation between fragmentation of the rice habitat and the predator group. On the contrary, the abundance of a predatory ladybird (*Micraspis* spp) increased with the number of rice patches. Ladybirds of the genus *Micraspis* feed on the eggs, nymphs and adults of a variety of pest insects. They are more abundant during outbreaks of _N.lugen_s and during rice flowering when they also feed on rice pollen (Pathak and Khan, 1994). In asynchronous cropping systems, fragmentation of the rice habitat can increase the occurrence of rice crops at different stages (e.g. flowering stage vs. temporarily unused fields), thus smaller rice habitat patches coupled with asynchronous rice fields could enhance mobile predator populations such as *Micraspis* spp. Indeed, it has been shown that arthropods can better colonize rice fields when the rice habitat is a mix of different rice crop stages or interspersed with other crops (Wilby et al., 2006). Mobile predators migrating between fields decreased pest densities more in asynchronous fields than synchronous ones, particularly if predators rapidly colonized newly planted rice fields (Ives and Settle, 1997). For example, the lycosid *P.pseudoannulata*, that inhabits rice bunds during fallow periods, is one of the first natural enemies found in newly established rice crops (Sigsgaard, 2000). In contrast, long-jawed orb-weaver spiders (family Tetragnathidae), which require tall foliage to suspend their webs, cannot rapidly recolonize rice fields (Barrion and Litsinger, 1994). This is also supported by my data where orb-weaver spiders were the only predator species negatively impacted by fragmentation of rice habitat in this study.

Complexity in the shapes of crop patches has rarely been addressed in studies focusing on arthropods. While patch shape can influence host finding for herbivores (Stanton, 1983), I found no significant relationships between herbivores and shape complexity in this study. On the other hand, the abundance of highly mobile predators and chironomids declined when the shapes of rice patches increased in complexity. As patches become more irregular, the perimeter-area relation of the patches changes considerably. For example, Grez and Padro (2000) showed that coccinellids in Chile emigrated less from square patches (simple shape with a low perimeter-area ratio) than rectangular patches (more complex shape with a high perimeter-area ratio) of wild cabbages. It was suggested that coccinellids are more likely to emigrate and abandon the more complex shapes because of the accessibility of alternative habitats and prey. In contrast, in this study the parasitoids from the genus *Oligosita* were more abundant in complex patch shapes where the perimeter-area ratio was higher, suggesting that the edge effect of field margins is important for parasitoids in rice fields. Such a factor could also determine the success of interventions such as ecological engineering.

The scale at which arthropods responded best to the landscape metrics varied among functional groups and species and partly reflected their dispersal abilities. Detritivores/tourists and predator groups mostly live at the base of the rice plants and are either wingless (collembollans, spiders) or limited in flight (chironomids). Thus, the scale at which they responded (100 m and 200 m) is expected to be lower than for highly mobile flying arthropods such as parasitoids (300 m). Some rice herbivores such as delphacids exhibit a physical dimorphism with a fully winged “macropterous” form and a truncate-winged “brachypterous” form (Heong and Hardy, 2009). The macropterous delphacids can colonize and disperse to multiple habitat patches and thus could be the reason why herbivores responded to the landscape metrics at a larger scale (300 m). While the long-jawed orb-weaver spider (Tetragnathidae) has low mobility, it still responded to the number of patches at a broad scale (300 m). However, a buffer of 100 m might not be enough to capture the fragmentation of the rice habitat, and thus, arthropods may respond to this landscape metric at broader scales only.

### 4.4.2 Trophic interactions

The predator group showed a strong numerical response to prey density. The abundances of predators were associated with a higher abundance of both herbivores and detritivores/tourists. In this study, spiders represented most of the predator group and have been noted to respond numerically to prey density (Riechert and Lockley, 1984; Kenmore et al., 1984). In the early stages of the rice plant, when the abundance of herbivores is low, detritivores act as an alternative prey for generalist predators (Settle et al., 1996; Gurr et al., 2016). Kenmore et al. (1984) suggested that a greater availability of food for predators could lead to an increase of the predators’ fitness leading to more offspring, lower competition, and higher survival of smaller individuals. The absence of a density-dependent relationship between parasitoids and herbivores can be explained by the sampling methods I used in this study. In a previous study, Horgan et al. (2017) showed that despite the lack of numerical response of parasitoids to herbivores in rice fields, egg parasitism was still density dependent. My sampling method did not measure egg abundance as a determinant of parasitoid abundance (i.e., parasitoid individuals remaining in larval stages inside the eggs or larvae of herbivores), and thus parasitoids sampled at the adult life stage may not have responded to prey the same way as generalist predators. Indeed, predator populations were largely driven by the availability of prey, likely masking any effects of landscape heterogeneity.

### 4.4.3 Synthesis and applications

This study shows, for the first time, that the combined effects of landscape heterogeneity and trophic interactions shape arthropod communities in rice agro-ecosystems. Fragmentation of the rice-production habitat is expected to increase production costs particularly since it constrains mechanization (Kawasaki, 2010); however, it can be beneficial for farmers, as it limits the risks of pest outbreaks, particularly if the production costs are not considerably higher than the ecosystem services it provides (i.e., weed and herbivore control). This study provides evidence that increasing the landscape diversity surrounding rice fields and increasing the number of rice patches can result in lower herbivore abundance. The bunds interconnecting rice fields are an important feature for parasitoids and predators, and more studies should focus on the potential functional connectivity of bunds in enhancing natural enemies particularly as a factor in the success of interventions such as crop diversification and ecological engineering. Manipulating the landscape to create a mosaic of rice fields with different temporal and spatial compositions and configurations could also provide natural enemies with a continuous availability of food. Arthropods with low dispersal ability such as spiders may benefit from the high availability of prey in the neighboring patches at a small scale, while flying arthropods with high dispersal ability such as parasitoids may benefit from the configuration of the landscape at larger scales. Based on these findings I recommend that landscape management to improve biodiversity and biological pest control in rice agro-ecosystems should promote a diversity of land uses and habitat types within at least 100-300 m radii, maintain smaller rice patches and enhance the structural connectivity of rice bunds.

This study was conducted in a real agricultural setting in which land management factors, such as pesticide input or cropping synchrony, were not controlled. Management practices and to a larger extent the use of insecticides can potentially disrupt the predator-prey relationships and the food web structure, ultimately leading to the loss of arthropod biodiversity and the reduction in the agro-ecosystem resilience to pest outbreaks (Kenmore et al., 1984; Heong et al., 1991; Way and Heong, 2009; Horgan and Crisol, 2013). In a previous study (Dominik et al. 2017), I have shown that management effects are potentially important in determining the arthropod composition in the study areas but that they vary between regions, while being relatively homogeneous within regions. Although these regional-scale effects cannot be fully disentangled from the effects of landscape heterogeneity, in this study I indirectly accounted for them by the nested design of my analyses. To further unravel the effects of landscape heterogeneity on arthropod communities, future research should directly address management practices and land-use intensity as additional factors potentially shaping rice arthropod communities. In addition, future research should focus on the effects of temporal and spatial manipulation of the rice habitat, and on the potential benefits of coupling small rice patches with large ones to better understand the effects of fragmentation in rice agro-ecosystems.

# Chapter 5

# Landscape heterogeneity filters arthropod traits in rice agro-ecosystems

## 5.1 Introduction

Asian tropical rice agro-ecosystems are represented by a mosaic of complex spatial patterns of rice crop, arthropod species (Dominik et al., 2017), plant species (Fried et al., 2017), and land use types (Settele et al., 2015). Biodiversity within the rice fields is often higher than in many natural ecosystems (Pimentel, 1992; Schoenly et al., 2010; Dominik et al. 2017). The resulting heterogeneity of these landscapes has important effects on agro-ecosystem processes by determining the distribution, dispersal, and interactions of the system biodiversity (Fahrig, 2003; Kremen et al., 2007). Landscape heterogeneity represents the combination of landscape composition (diversity of landscape features and habitat types) and landscape configuration (number, size, and connectivity of habitat patches) (Seppelt et al., 2016), and is known to influence the distribution of species within a community (Turner, 1989; Fahrig et al., 2011). The composition of the landscape influences biodiversity as more heterogeneous landscapes (containing a larger variety of different cover types) provide more habitats for species (Benton et al., 2003; Tscharntke et al., 2005; Devictor and Jiguet, 2007). For example, increasing non-crop habitat in rice via habitat manipulation has proven beneficial for some natural enemies of rice pests (Gurr et al., 2016). On the other hand, the configuration of the landscape may positively affect biodiversity by increasing landscape complementation (i.e. where resources within the landscape are not substitutable) (Fahrig et al., 2011) via influencing species movement and spill overs (Tscharntke et al., 2005; Blitzer et al., 2012). In Dominik et al. (2018), I showed that some natural enemies of rice pests responded positively to increased configurational heterogeneity (measured as number of rice patches and connectivity of the terrestrial levees separating the rice patches). However, it is still unclear which specific species respond to landscape heterogeneity in agro-ecosystems.

The impacts of environmental change on arthropod biodiversity in rice agro-ecosystems have traditionally been investigated using a taxonomic approach by focusing on the distribution of species within a community or by sorting species into functional groups (Heong et al., 1991; Schoenly et al., 2010; Dominik et al., 2017). However, these approaches have failed to take into consideration the variability of species within functional groups, especially when comparing different regions with different species communities (McGill et al., 2006). In recent years, research on the responses of species functional traits to environmental change has received increasing attention (Kleyer et al., 2012; Duflot et al., 2014; Gàmez-Virués et al., 2015). Such studies aim to understand whether species with certain traits will persist under specific environmental conditions (Southwood, 1988; Townsend et al., 1997). The functional characteristics of a species (i.e. species traits) influence its dispersal, resource acquisition, reproduction and resilience in the environment (Violle et al., 2007; Pavoine and Bonsall, 2011). Species differ in their response to environmental factors and ecosystem functioning. For example, predator assemblages exhibiting a high diversity in functional traits are likely to have similar traits associated with prey capture and consumption (Petchey and Gaston, 2002). In their review, Gagic et al. (2015) showed that functional trait indices are indeed superior to taxonomic indices in linking diversity to ecosystem functions, including pollination and biological control. The environment can act as an ecological "filter" that selects or excludes species from the regional pool according to particular functional traits (Southwood, 1988; Townsend and Hildrew, 1994; Poff, 1997). Similarly, landscape heterogeneity may also be considered as an ecological filter (Tonn et al., 1990; Duflot et al., 2014). In a recent study in Germany, Gàmez-Virués et al. (2015) showed that landscape-level effects are critical for maintaining functionally diverse communities, by providing resilience and stability of functional traits to buffer the negative effects of land-use intensity. By measuring both components of landscape heterogeneity, Duflot et al. (2014) demonstrated the filtering effects of landscape heterogeneity on carabids and plants functional traits in temperate agricultural areas.

Most of the previous studies examining trait-environment relationships have focused on temperate ecosystems (Duflot et al., 2014; Gàmez-Virués et al., 2015). Moreover, I am unaware of any studies examining the relationships between arthropods traits and environmental variables in rice agro-ecosystems. In this study, I investigated the distribution of arthropods traits along a gradient of landscape heterogeneity in the rice agro-ecosystems of the Philippines across multiple regions. I focused on body size, dispersal ability, functional groups, specialization and vertical stratum, which are recognized as important ecological traits (Schweiger et al., 2005; Gossner et al., 2013; Simons et al., 2016). The following hypothesis were proposed: (1) landscape heterogeneity (composition and configuration) acts as an environmental filter for rice-arthropods, and (2) landscape heterogeneity filters specific functional traits.

## 5.2 Materials and methods

### 5.2.1 Study regions

The study was conducted across three 15 x 15 km regions on the island of Luzon in the Philippines as described in 2.1.1. The three regions were: (i) a rice landscape in the hilly lowlands of Laguna Province in southern Luzon (PH_1); (ii) an intensively cultivated rice landscape in Nueva Ecija Province (PH_2) situated in central Luzon ; and (iii) a traditional terraced rice system in the mountainous Ifugao Province located in the north of Luzon (see Klotzbücher et al., 2015; Dominik et al., 2017). Within each region, five pairs of fields (i.e. 10 “core sites”) were selected for a total of 28 core sites (sampling could not be performed at two core sites in PH_2 due to the presence of planted vegetables instead of rice at the time of sampling). The average distance between two cores sites was ~ 369 m.

### 5.2.2 Arthropod sampling

The rice arthropods were collected using a modified leaf blower-vacuum during the dry season of 2013 in PH_1 and PH_2 and during the single cropping season of 2014 in PH_3 as described in 2.3.1. All samples were collected at the maximum tillering stage of the rice plant (50 days after transplanting) to ensure consistency of sampling; this stage being generally associated with a maximum abundance of arthropods (Heong et al., 1991; Wilby et al., 2006).

Collected arthropods were preserved in 70% ethanol, sorted and identified to species level (or morphospecies level when species level was proven too difficult) using a binocular microscope and based on the taxonomic keys of Barrion and Litsinger (1994). Morphological similarity at the pre-adult stages and quality of the samples limited the identification of arachnids, dipterans and collembolans to family level.

### 5.2.3 Landscape heterogeneity

Landscape heterogeneity was quantified by calculating three independent metrics of landscape composition and configuration. All landscape metrics were identified and mapped within a 300-m radius around each core site using GIS-Software (ArcGIS 10.3, ESRI) and high-resolution SPOT-5 DIMAP images (2.5 m) as described in 2.2.1. Land cover features were classified into eight final categories: rice fields, woodlands, grasslands, artificial areas, plantations, rice bunds, hydrographic network, and ponds.

I used Shannon's Diversity Index (SHDI) as a measure of compositional landscape heterogeneity. SHDI was calculated based on all eight land cover categories. I used two metrics to represent the configurational landscape heterogeneity of the rice habitat. The rice agro-ecosystem is usually composed of several rice fields (typically 1-3 ha in size) interconnected by a network of terrestrial levees (rice bunds). First, I calculated the number of rice patches (NP) as a measure of fragmentation of the rice habitat. The fragmentation of the rice habitat (NP) represents the breaking apart of the rice habitat, subdividing a single rice patch into numerous smaller patches of rice. Rice terraces found in the mountainous regions are comprised of a mosaic of rice patches that greatly differ in size and shape. In contrast, monocultures of rice fields in the lowlands are often large and of rectangular shape to facilitate agriculture intensification. Thus, I additionally calculated the core area index (CAI) for each rice patch to quantify the percentage of the patch comprised of interior area (rice) based on a 1-m edge effect (bund). For example, a large rice patch of rectangular shape will have a higher core area index than a small rice patch of irregular shape. The CAI isolates the configuration effect since it is more an edge-to-interior ratio like many of the shape metrics. Both NP and CAI metrics were not correlated with each other ($r = -0.23$ $p = 0.25$).

All landscape metrics were calculated using Fragstats 3.3 (McGarigal and Marks, 1995).

### 5.2.4 Arthropods traits

Trait information was obtained from the literature and expert opinion for all species identified in this study (Barrion and Listinger, 1984; Heong and Hardy, 2009; Pathak and Khan, 1994; Horgan pers. Comm.). Trait information at the genus or species level was used when data was available, otherwise subfamily or family level information was used (for Chironomidae and arachnids). Five traits were selected related to body size, dispersal ability (wing dimorphism), functional group, specialization (generalist or specialist), and vertical stratum (see Appendix

K).

(1) Body size was defined as the mean body length in mm for both sexes. Body size is related to many life-history traits such as fecundity, life span, and growth rate.

(2) Dispersal ability was classified in three groups according to the flying capability of the species. All flightless species (apterous) were classified as a very low dispersal group. Species displaying wing dimorphism in adult stage were assigned as a medium dispersal group. For example, the brown planthopper *Nilaparvata lugens* can exhibit both the fully winged "macropterous" and truncate-winged "brachypterous" forms. Their wing dimorphism is mostly determined by food availability in the nymphal stage of the corresponding generation. While the brachypterous forms generally infest the rice fields, the macropterous forms are responsible for colonizing new fields when food becomes scarce. Finally, fully winged species ("macropterous") were classified as a high dispersal group.

(3) Functional group was classified based on the diet of each species during the adult stage. The different categories were as follows: (i) herbivores; (ii) predators; (iii) parasitoids; and (iv) detritivores (following Moran and Southwood 1982).

(4) Specialization was defined as the niche breadth of the species. Generalists were classified as species feeding on multiple different species (such as spiders). Specialists were classified as species feeding on one or very few species (such as planthoppers).

(5) Vertical stratum was defined as the main vertical habitat layer in which the species was usually observed as an adult. I distinguished between water bodies, base of the rice plant, and rice-canopy.

### 5.2.5 Statistical analyses

Abundance of arthropods was standardized across all taxa using Hellinger transformations to account for regional differences in environmental gradients across the three regions (Dominik et al., 2017). The relationships between rice-arthropods traits and landscape heterogeneity was investigated by the combination of RLQ (Dolédec et al., 1996) and fourth-corner analyses (Legendre et al., 1997).

RLQ analysis was used to test the first hypothesis that landscape heterogeneity acts as an environmental filter of rice arthropods. RLQ analysis is an extension of the two-table method for co-inertia analysis (Dolédec et al. 2006) that allows for the simultaneous analysis of three tables: an environmental table (named R: landscape metrics x sites), a species traits table (named Q: species x arthropods traits), and a species abundance table (named L: species x sites) that is used as the link between Q and R. It is a special form of correspondence analysis used to investigate the main co-structures between traits and environmental variations mediated by species abundance. Prior to the analyses and after selecting the species occurring in at least 15 % of the sites (i.e. 54 species), species abundance table was subject to a correspondence analysis (CA) as recommended. Then, principal component analysis (PCA) were performed on the trait and environmental tables (the Q-table using the Hill and Smith method for mixing quantitative variables and factors) by considering species and sites weights derived from the correspondence analysis species scores. The final co-structure between traits and landscape heterogeneity was then decomposed onto the different axes of the RLQ analysis. The prevailing co-correlation between arthropod traits and landscape metrics is defined by the first axis, and each successive axis summarizes the remaining co-correlation. The overall significance of the relationship between species traits and the normed scores of the first two axes of the RLQ analysis was further assessed via a Pearson rank correlation test. The same test was performed to assess the significance of the link between landscape metrics and the normed scores of the first two axes of the RLQ analysis. Following Kleyer et al. (2012), cluster groups were identified based on Euclidiean distances between species along the first two RLQ axes and clustered via Ward's hierarchical clustering. To determine the optimal number of clusters, Calinski-Harabasz stopping criterion was used.

In addition, a partial-RLQ analysis was performed to test the potential effect of the "region" covariates, where the covariable represents a partition of samples into groups (in this case the groups are the three regions PH_1, PH_2 and PH_3). Based on Wesuls et al. (2012), the percentage of co-inertia explained by the most representative axis of partial-RLQ was compared with the axis of the basic-RLQ. The influence of the covariate is relevant if the percentage of co-inertia explained by the axis of partial-RLQ were to be much higher than in the basic-RLQ.

To test the second hypothesis and further explore the relationships between species traits and landscape heterogeneity, a fourth-corner analysis was performed (Dray and Legendre, 1998). The fourth-corner analysis method was used for statistical power by testing the correlation between each arthropod trait and each landscape metric. Because of the multiple testing of three landscape metrics, a Bonferroni correction was applied to the alpha level (0.05/3 = 0.0166). The combined use of permutation models requires the square root of the corrected alpha level (Dray and Legendre, 2008; Gallardo et al., 2009). Therefore, I used square root of 0.0166 = 0.129 as levels of significance.

All statistical analyses were performed using the open source R software version 3.3 (R Core Team, 2016). I used the library vegan (Oksanen, 2011) for the cluster analysis and Hellinger transformations, and the library ade4 (Dray and Dufour,

2007) for both the RLQ and fourth-corner analyses.

## 5.3 Results

The first two axis of the basic-RLQ explained 92.97% of the total variation, whereas those of the partial-RLQ explained 98.74% (Table 5.3.1). The percentage explained by the first axis of the partial-RLQ was hardly higher than the percentage explained by the first axis of the basic-RLQ (72.4% and 71.4%, respectively), meaning that the scores of both landscape metrics and arthropod traits on the first axis of the basic-RLQ were not influenced by the effect of regions. Therefore, only the results of the basic-RLQ were described and reported in the text.

Landscape diversity (SHDI) and the number of rice patches (NP) were highly correlated with the first RLQ axis (Table 5.3.1). This axis mainly separated the sites with low landscape diversity (SHDI) and high number of rice patches (NP) from the sites with high landscape diversity (SHDI) and low number of rice patches (NP). Thus, the first RLQ axis represented a gradient of landscape diversity (SHDI) from left to right and a gradient of fragmentation of the rice habitat (NP) from right to left. The second axis, even if less pronounced than the first axis, showed an ecological gradient dominated by the core area of rice (CAI) followed by the number of rice patches (NP) and landscape diversity (SHDI), clearly separating the small irregular patches of rice from the large and regular patches of rice. These two gradients of landscape heterogeneity supported the first hypothesis that landscape heterogeneity acts as a filter for rice-arthropods.

| | | **1st Axis (71.4%)** | **2nd Axis (21.8%)** |
|---|---|---|---|
| **Environmental variables** | | | |
| | SHDI | **0.86** | **-0.47** |
| | NP | **-0.68** | **-0.59** |
| | CAI | -0.28 | **0.87** |
| **Arthropod Traits** | | | |
| | Body Size | **-0.39** | **-0.52** |
| | Functional group | **0.79** | **0.87** |
| | Dispersal ability | **0.77** | **0.31** |
| | Vertical stratum | 0.08 | **-0.44** |
| | Specialization | **0.65** | **0.67** |

**Table 5.3.1:** Results of the basic RLQ analysis and correlation between landscape metrics and the RLQ axes. Significant correlation values ($p < 0.05$) are highlighted in bold.

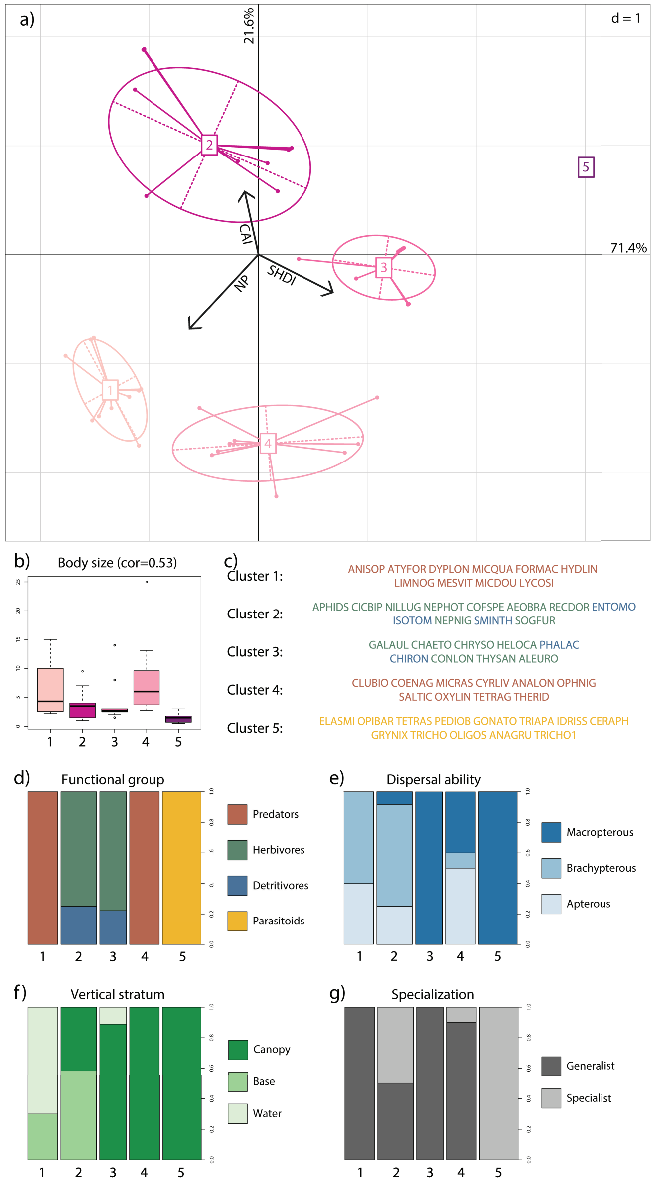


**Figure 5.3.1:** RLQ biplot showing the decomposition of co-correlations between landscape variables and trait variables, constrained by abundance of arthropods. The size and direction of environmental effects are represented by arrows. Identified clustered groups are represented with the same color (a). The boxplot represents the body size attribute for each cluster (b). Species attributed to each cluster are listed and colored based on their functional group (NOT their cluster group) (c). The width of the bars represents the relative abundance of each cluster to the corresponding functional trait and its proportion is represented by the height of the bar (d-g).

All arthropods traits were significantly associated with the two RLQ axes, meaning that species abundances were influenced by arthropod traits except for the vertical stratum that showed no association with the first RLQ axis (Table 5.3.1). Additionally, five clusters based on the mean position of each species on both

RLQ axes were identified via hierarchical cluster analysis (Figure 5.3.1). Cluster 1 was comprised of generalist predators living in both water bodies and at the base of the rice plant, and mostly occurring in highly fragmented rice habitats (NP). Cluster 2 grouped the herbivores and detritivores (collembollans) living both at the canopy and the base of the rice plant. Additionally, arthropods from cluster 2 were found in large rice patches of regular shape (CAI). Cluster 3 included highly mobile generalist herbivores and detritivores visiting exclusively the canopy of the rice plant. Unlike cluster 2, they were more likely to be found in sites with high landscape diversity (SHDI). Cluster 4 was mostly comprised by generalist predators found at the canopy of the plant and displaying multiple degrees of dispersal. Like cluster 1, they shared a larger body length than other clusters, and preferred rice habitats with small and irregular patches (CAI). However, this cluster comprised species favouring both highly fragmented rice habitats (NP) and highly heterogeneous sites (SHDI). Finally, the cluster 5 was comprised of small specialist parasitoids, which are mostly found at the canopy of the plant and have high dispersal ability, and was associated with sites with high landscape diversity (SHDI).

The second hypothesis that landscape heterogeneity influences specific arthropod traits was supported by the fourth-corner analysis. Indeed, the fourth corner analysis detected significant associations between arthropod traits and landscape heterogeneity metrics (Table 5.3.2). Highly fragmented rice habitats (NP) favoured predators and apterous species. In contrast, parasitoids, macropterous species, and species preferring the canopy of the plant showed the opposite response to the fragmentation of the rice habitat (NP). Landscape diversity (SHDI) was most positively associated with parasitoids, macropterous species and species occurring at the canopy of the plant. Brachypterous species and species living at the base of the rice plant were negatively correlated with landscape diversity (SHDI). Finally, the core area index (CAI) was negatively correlated with predators.

## 5.4 Discussion

The findings of this study allowed me to assess the importance of both landscape composition and configuration as filters of rice arthropods traits composition. The two main gradients representing landscape diversity (composition of the landscape) and fragmentation of the rice habitat (configuration of the landscape) pointed in opposite directions; hence heterogeneous rice landscapes (SHDI) tend to have less

| | | Landscape heterogeneity | | |
|---|---|---|---|---|
| | | **Landscape composition** | **Landscape configuration** | |
| | | SHDI | NP | CAI |
| **Body size** | | | | |
| **Dispersal ability** | | | | |
| | Macropterous | + | - | |
| | Brachypterous | - | | |
| | Apterous | | + | |
| **Functional group** | | | | |
| | Predators | | + | - |
| | Herbivores | | | |
| | Detritivores | | | |
| | Parasitoids | + | - | |
| **Specialization** | | | | |
| | Specialist | | | |
| | Generalist | | | |
| **Vertical stratum** | | | | |
| | Canopy | + | - | |
| | Base | - | | |
| | Water | | | |

**Table 5.3.2:** Four Corner analysis of the effects of landscape heterogeneity on arthropod traits. Positive correlations between arthropod traits and landscape metrics are represented by the symbol + and negative correlations are represented by the symbol -. Only significant results (p-values $< 0.129$) are reported.

fragmented rice habitats and vice versa. Additionally, a third gradient separated the large and regular rice patches found in the lowlands (PH_1 and PH_2) from the irregular and smaller rice patches of the mountainous region (PH_3). The third gradient was mainly represented by a gradient of size and shape of the rice patches (CAI) which pointed in the opposite direction of the fragmentation of the rice habitat (NP) and landscape diversity (SHDI) gradients. Thus, the mountainous region of PH_3 was characterized by highly heterogeneous sites (SHDI) subdivided in multiple smaller rice patches (NP) of irregular shape (CAI). On the other hand, the lowlands regions of PH_1 and PH_2 were characterized by homogeneous landscapes (SHDI) comprised of larger but fewer rice patches (NP) of regular shape (CAI). Hence, landscape heterogeneity, represented by the combination of the three gradients (SHDI, NP, and CAI), influenced the rice arthropod community according to their functional group, dispersal ability, and the vertical stratum of the arthropods. While previous studies have demonstrated the importance of landscape variables as filters of arthropod trait composition in temperate habitats (Duflot et al., 2014; Gàmez-Virués et al., 2015), the present study is the first to detect these relationships in tropical rice agro-ecosystems.

Landscape heterogeneity had a strong filtering effect on the dispersal ability trait of the rice-arthropod community, clearly separating the apterous species (low dispersal ability) from the macropterous species (high dispersal ability). Highly fragmented rice habitats (NP) and low heterogeneous landscapes (SHDI) selected predator species with low dispersal ability (apterous and large), which mostly inhabit the base of the plant or water bodies. In the current study, the apterous species were mostly represented by the clusters 1 and 2, which comprised generalist predators such as spiders and aquatic species. Thus, these results showed a similar trend found in Gàmez-Virués et al. (2015) where generalist species with relatively large body sizes were favoured in simplified landscapes. In addition, Dominik et al. (2017) showed that predators were found in higher numbers in low heterogeneous sites in the lowlands of the Philippines. In contrast, Duflot et al. (2014) found that large and low mobility carabid beetles in temperate agricultural landscapes were associated with high diversified landscapes (measured as proportional area of non-crop land). In these diversified temperate landscapes, species may use a combination of annuals crops and woody habitats, and benefit from edges between habitats, strongly suggesting an effect of habitat supplementation (i.e. where resources within the landscape are substitutable) (Tscharntke et al., 2005). In the current study, the fragmentation of the rice habitat (NP) into numerous smaller rice patches had a positive effect on low mobility predator species. Rice habitat being held constant, increasing fragmentation implies smaller distances between patches, which reduces habitat isolation and facilitates immigration of low mobility species (Fahrig, 2003). Additionally, more fragmented habitats generally contain more edge, which can have a positive effect on the distribution of certain species (Carlson and Hartman, 2001; Laurance et al., 2001; Fahrig, 2003). Additionally, more fragmented rice habitat might have a higher level of interdigitation of different habitat types, increasing both landscape complementation and supplementation for these species (Dunning et al., 1992). Increasing the number of rice patches - irrespective of habitat loss - can increase the probability of crop types and/or different rice crops at various temporal stages, which are known to alter the community of rice arthropods (Wilby et al., 2006; Schoenly et al., 2010). Indeed, two key spider species in rice, *A. formosana* and *P. pseudoannulata* are known to use the different rice habitats as alternative food resources (set-a-side rice field, edge of bund, crop at different stage of the plant, etc.) (Barrion and Litsinger, 1984) and are among the first natural enemy species to colonize newly planted rice fields (Sigsgaard, 2000). For aquatic species of rice that depend on the amount of water available in each rice patch, the proximity of other irrigated rice patches will determine the facility to which these aquatic species may easily move among the rice habitat. However, landscape composition may have different effects depending on whether composition is perceived as heterogeneity or disturbance by the studied functional groups (Tews, 2004). Indeed, while the results showed a positive effect of fragmentation of the rice habitat (NP) on low mobility predators, the opposite trend was found for fully winged parasitoids.

Less fragmented rice habitats (NP) and highly heterogeneous landscapes (SHDI) favoured species with high mobility dispersal (macropterous), mostly found at the canopy of the rice plant. These landscapes offer a greater variety of habitats, which may provide additional resources (e.g. shelter, alternative or complementary food sources) (Landis et al., 2000). Parasitoids are among the most important natural enemies of planthoppers in rice and their parasitism rates can range from 32% and 42% in Philippine rice fields (Kenmore et al., 1984). Their high dispersal ability allows them to travel over great distances in search for suitable hosts (Antolin and Strong, 1987). By increasing the diversity and density of nectar flowering plants along the rice bunds, Gurr et al. (2016) found higher abundances of parasitoids in enhanced rice habitats than in conventional rice habitats across sites in China, Thailand and Vietnam. Similarly, positive effects of non-crop habitats on the abundance of the parasitoid *Anagrus* spp. have already been established in rice (Gurr et al., 2011; Zhu et al., 2013). However, several authors showed no evidence that flowering strip could promote parasitoid populations at the field scale (Lin et al., 2011; Yao et al., 2012; Horgan et al., 2017). In addition, a study on four hopper parasitoid genera found that parasitoids were significantly less abundant in agroforests than in rice habitats (Sann et al., 2018). However, it is important to note that in the papers previously mentioned, landscape heterogeneity was measured at different scales (field or landscape scale) and sometimes with simplistic quantification of the landscape (rice habitat vs agroforest). Thus, these sometimes contrasting results demonstrated the complex responses of parasitoids to landscape heterogeneity in rice agro-ecosystems.

Finally, landscape diversity (SHDI) was negatively associated with species displaying intermediate dispersal ability (brachypterous), i.e. homopterans and most of the aquatic predators. While landscape diversity (SHDI) has been shown to reduce the abundance of herbivores in the Philippines, especially planthoppers (Dominik et al., 2018), I did not find any effect of landscape diversity on herbivores as a functional group. However, the RLQ analysis successfully separated brachypterous herbivores from macropterous herbivores on the landscape heterogeneity gradient. Polyphagous fully winged arthropods such as *Chaetocnema* spp and *Conocephalus longivipennis* have a wide range of hosts (Heinrichs et al., 1982) and may benefit from the non-crop habitats by visiting alternative food sources when rice is absent. On the other hand, monophagous homopteran rice pests such as *Nilaparvata lugens* and *Nephotettix* spp. feed primarily on rice (Heinrichs and Medrano, 1984) and are among the most devastating rice pests in Southeast Asia (Lin et al., 2011). Therefore, homopteran rice pests depend less on non-crop habitats and are more likely to show a positive density-area relationship in rice habitat (Hambäck et al., 2007; Dominik et al., 2018). Hence, by selecting traits that are important in describing life history strategies, these findings showed that landscape heterogeneity can have multiple and contrasting filtering effects on the same functional groups (i.e. herbivores). Additionally, similar trends were observed for different functional groups (parasitoids, predators, and herbivores), thus indicating that landscape heterogeneity acted as a strong filter on the dispersal ability at the landscape level and could be potentially generalized to other taxonomic groups.

The third gradient played a lesser role in filtering rice-arthropod traits, but selected mostly against predators in large and regular rice fields (CAI). Small and irregular patches (CAI) favoured predators independently of the vertical stratum or dispersal ability in the current study. Both of the clusters grouping exclusively predators displayed the largest body size. While the results of the fourth-corner analysis did not show any significant effect of landscape metrics on body size, larger body size is generally expected to be related to smaller size patches, since larger species can better disperse between smaller, more isolated, patches (Gàmez-Virués et al., 2015). These results are thus in agreement with Settle et al. (1996), who demonstrated that large monocultures of rice delayed the colonization by predators in Indonesia. Additionally, the gradient of landscape intensity separated the intensive rice fields of the lowlands (PH_1 and PH_2) from the traditional rice fields of the uplands (PH_3), suggesting that predators were more dominant in less intensive rice fields. In contrast, prey species represented by the cluster 2 were observed at the opposite end of the configurational landscape gradient, favoured by the more intensive rice fields of the lowlands. The present study was conducted in a real agricultural setting in which agrochemical inputs such as pesticides and fertilizers were managed by the farmers and not controlled, except for the pesticide free mountainous region (PH_3). The negative impact of insecticide applications on the biological control potential by either direct killing of natural enemies or by disrupting food chains has been largely acknowledged (Heinrichs et al., 1982; Heinrichs and Mochida 1984; Cohen et al., 1994; Schoenly et al., 1996; Heong and Schoenly, 1998). Therefore, while these findings showed that the third gradient filtered functional groups based on three different landscape metrics (NP, SHDI and mostly CAI), they also suggested that other factors than landscape heterogeneity such as land management practices (e.g. insecticide applications) may play a key role in the distribution of the rice-arthropod community (also see Dominik et al., 2017). In that regard, this third gradient, as a measure of configurational heterogeneity, was possibly cofounded with the effects of local management and land-use intensity in these sites. Indeed, agriculture in the lowlands is generally associated with increased use of chemical inputs (i.e. pesticides, fertilizers, etc) and mechanization farming systems over large monocultures of rice, whereas the size of the rice patches in the mountainous region are too small and inaccessible for mechanization. Furthermore, farmers in the lowlands have better access to high yield varieties and chemical inputs, while rice-farming systems in the mountainous region rely more on traditional rice varieties and less chemical input.

From a policy perspective, the landscape heterogeneity filtering effects showed that both parasitoids and predators had distinct and contrasting habitat requirements. Thus, the results of this study indicated that not all functional groups can be preserved at the same time. On one hand, highly fragmented rice habitats (NP) provided a more suitable habitat for predators with low mobility. On the other hand, highly heterogeneous sites (SHDI) promoted macropterous species living at the canopy of the rice plant, e.g. parasitoids. By breaking the rice habitat into smaller patches of rice, predator populations increased while herbivore populations decreased. A higher number of rice patches at different stages of the rice plant (asynchronous farming) offers the advantage of creating continuous refuges for migrating arthropods (Bottrell and Schoenly, 2012). Increasing the number of patches could also promote intercropping (or polycropping), where fewer planthoppers (49-55%) have been recorded (Lin et al., 2011), which ultimately leads to an increase of landscape diversity within the rice habitat itself. While landscape diversity (SHDI) was measured as the diversity of non-crop habitats surrounding the rice fields (woodlands, artificial areas, etc.), the diversity of the rice habitat itself (crop at a different stage of the plant, abandoned rice field, ratton crop, different crop, etc.) was not considered. My methods did not capture the diversity of the rice habitat as a measure of landscape composition. However, by increasing the number of rice patches (NP), the diversity of the rice habitat may also increase; hence highly fragmented rice habitats potentially harbor a more diverse rice habitat. Thus, asynchronous planting coupling with intercropping could provide natural enemies with a continuous source of food and refugia. Therefore, via temporal and spatial manipulation of the rice habitat, future research should focus on identifying thresholds of landscape heterogeneity between fragmentation and landscape diversity gradients that offer the most suitable habitat for both parasitoids and predators, the natural enemies of herbivores pests in the rice fields.

## 5.5 Conclusion

I used RLQ analyses together with fourth-corner permutation tests to study rice-arthropods traits across a landscape heterogeneity gradient. Additionally, I demonstrated the role of landscape heterogeneity as an ecological filter of rice-arthropods in relation to their dispersal ability, functional groups, and vertical stratum. These results suggest that both the composition and configuration of the landscape select against different functional groups. Hence, future studies should focus on finding thresholds of landscape heterogeneity supporting multiple taxa in the rice-fields. These findings support that multiple trait-based approaches may complement taxonomic approaches in large-scale studies.

# Chapter 6

# Synthesis, limitations and conclusion

The overall aim of this thesis was to identify the effects of different types and scales of landscape heterogeneity on the arthropod community in rice agro-ecosystems (see 2.4. Thesis outline). As part of this research I used a landscape ecology approach, and for the first time in rice agro-ecosystems, I tested the influence of both compositional and configurational heterogeneity on the diversity of rice arthropods. In addition, I did not limit the research questions to a single group of arthropods but focused on the most representative functional groups of rice agro-ecosystems, including herbivores and their natural enemies. In this final chapter, I summarized the overall findings from the multi-level approach to arthropod biodiversity and landscape heterogeneity that was used in the thesis; and discussed its implications for the enhancement of natural biological control at the landscape level. Finally, I addressed the limitations of the research design used in the previous chapters, and the potential that this research may offer for further investigations of sustainable rice production at the landscape level.

## 6.1 The drivers of arthropod community in rice agro-ecosystems

The results of the present thesis demonstrated the role of landscape heterogeneity in determining the arthropod community composition in rice agro-ecosystems. However, the effects of the two components of landscape heterogeneity (composition and configuration) varied among taxa. One of the main findings from the previous chapters showed the importance of landscape composition in reducing the presence of pest herbivores of rice (Chapters 4 and 5). However, increasing the compositional heterogeneity of the landscape did not necessarily enhance the diversity of natural enemies in rice (Chapters 3, 4 and 5). Yet the considerable variety of natural enemy species offered a sizeable variability of responses, either positive or negative, to the configurational heterogeneity of the landscape (Chapters 4 and 5). At last, the arthropod community in rice may be explained by additional factors other than landscape heterogeneity, such as regional-scale effects or strong density-dependence relationships (Chapters 3 and 4) (see Figure 6.1.1).

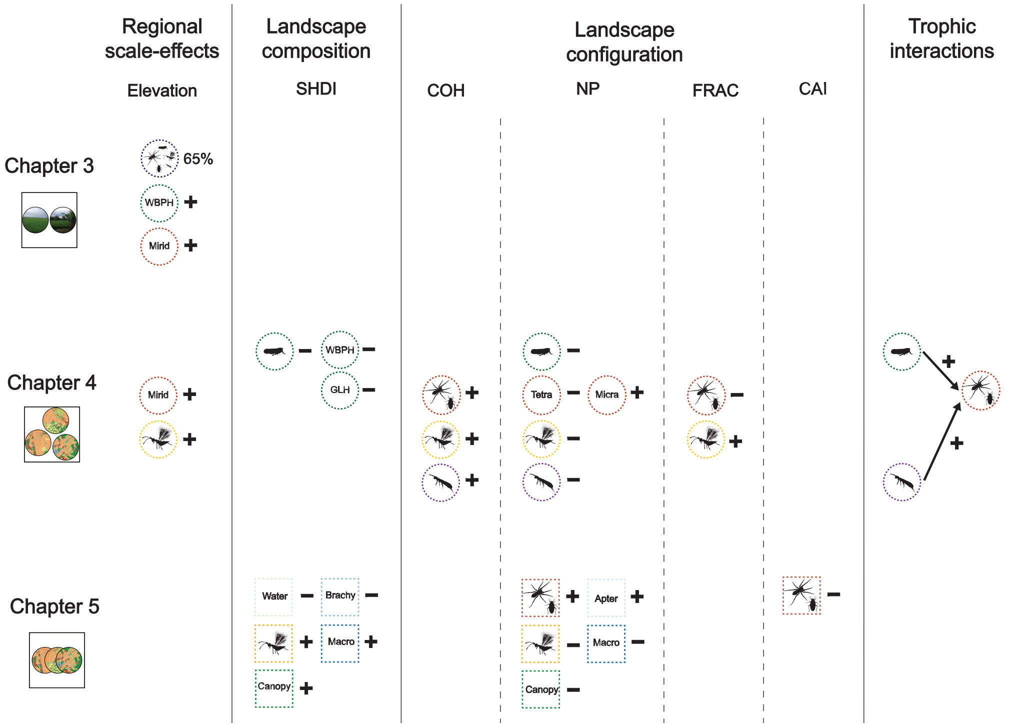


**Figure 6.1.1:** Overview of the main results of Chapter 3, 4 and 5. Positive correlations between arthropod abundance/traits and landscape metrics are represented by the symbol + and negative correlations are represented by the symbol -. SHDI = landscape diversity; COH = connectivity of the bunds; NP = fragmentation of the rice habitat; FRAC = shape complexity of the rice patches; CAI = core area index. Round borders represent arthropod abundance and rectangle borders represent arthropod traits. Green = Herbivores ; Red = Predators ; Orange = Parasitoids ; Purple = Detritivores/Tourists ; Blue circle = Assemblages. WBPH = *S.furcifera* ; Mirid = *C.lividipennis*; GLH = *Nephotettix* spp; Tetra = Tetragnathidae; Micra = *Micraspis* spp; Brachy = Brachypterous; Macro = Macropterous; Apter = Apterous.

### 6.1.1 Landscape composition can reduce the presence of rice pests

The benefits of landscape diversity for reducing herbivore abundance within rice fields were first demonstrated in Chapter 4 when responses of arthropods to landscape composition were measured within each region. The mixed modelling approach demonstrated that landscape diversity was significantly correlated with the decrease of herbivore abundance, including major pest species such as *S.furcifera* and *Nephottetix* spp.. Furthermore, the results of Chapter 5 showed that landscape composition negatively influenced species with intermediate dispersal ability (brachypterous species), which are mostly represented by homopterans herbivores such as *N. lugens*, *S. furcifera*, and *Nephottetix* spp.. These findings highlighted for the first time the positive effects of landscape diversity in reducing herbivore abundance in rice agro-ecosystems at the landscape level. Despite these promising results, the potential effect of natural biological control in heterogeneous landscapes was not established. Most natural enemies did not respond to the composition of the landscape in the early chapters (3 and 4), suggesting that the mechanisms underlying the reduction of herbivore abundance in heterogeneous landscapes could not be fully attributed to the increase of natural enemies. Only by identifying arthropod functional traits and measuring landscape diversity across all regions did I find that landscape with high compositional heterogeneity favoured parasitoids and to a further extent species with high dispersal ability (macropterous species) (Chapter 5). Although semi-natural habitats such as agro-forests did not allegedly enhance parasitoid abundances (Sann et al., 2018), the wild vegetation present in the ecotone between the rice habitat and non-rice habitat most likely benefit parasitoid populations. Highly mobile species feeding on nectar as an alternative source of food are usually more abundant near the edges of the crop than in the centers (Baggen and Gurr, 1998; Thies and Tscharntke, 1999). Indeed, higher abundances of parasitoids were reported when increasing the diversity and amount of nectar flowering plants along the rice bunds across multiple sites in China, Thailand and Vietnam (Gurr et al., 2016). More heterogeneous landscapes generally provide additional habitat and resources for both parasitoids and predators (Landis et al., 2000) but landscape diversity did not increase the presence of predators in the study systems (Chapter 4 and 5). In contrast to temperate regions, where natural and semi-natural habitats can provide overwintering sites with alternative prey and refuge for natural enemies (Rand et al., 2006), the spatial mosaic of tropical rice agro-ecosystems can ensure continuous availability of food for predators (Ives and Settle, 1997). These findings strongly suggest that the rice habitat itself provides more important resources for predators than non-crop habitats.

### 6.1.2 Landscape configuration facilitates the movement of natural enemies

The responses of arthropods to landscape configuration (measured as the number of rice patches, the connectivity of the rice bunds and the shape of the rice patches) greatly differed among the functional groups (Chapter 4 and 5).

Early crop colonization by natural enemies has been considered an important factor for successful biological control (Settle et al., 1996; Ives and Settle, 1997; Costamagna et al., 2015). By facilitating the movement of arthropods into neighbouring rice fields, the spatial arrangement of the rice habitat may promote the early arrival of natural enemies. Indeed, the connectivity of the rice bunds and fragmentation of the rice habitat affected the movement of species according to their dispersal ability (Chapter 4 and 5). However, dispersal ability is not a fixed trait and differed from one natural enemy species to another, which consequently impacted the responses of species to configurational heterogeneity (Chapter 5). For example, the bunds surroundings the rice fields acted as corridors in the fragmented rice habitats and enhanced parasitoid species richness and abundance in the study systems (Chapter 4). These linear landscape elements also favoured the presence of other functional groups such as predator species and detritivores abundance (Chapter 4). While increasing the connectivity between habitat patches may also promote crop pests (Margosian et al., 2009), none of the rice herbivores responded to the connectivity of the bunds in the analysis (Chapter 4). The suitability of these rice bunds as additional source of food, habitat and dispersal corridors for parasitoids could determine the success of ecological engineering applications to enhance biological control (Gurr et al., 2004; Gurr et al., 2016; Horgan et al., 2016).

Rice agro-ecosystems are characterized by a spatially fragmented landscape of rice fields but also by strong temporal changes in resource availability via asynchronous cropping. Rice habitats with smaller and more numerous fields may involve more frequent alteration of fields at different stages of the rice plant and management practices per field. Yet, management practices in rice fields such as field preparation, pesticide applications, and harvesting generate unstable habitats for arthropods. More specifically, the overuse of pesticides to control arthropod pests can disrupt the predator-prey relationships and the entire food web structure (Kenmore et al., 1984; Heong et al., 1991; Way and Heong, 2009). The results of Chapter 3 highlighted how important regional management effects can be in determining the arthropod composition in the study areas. Therefore, movement of arthropods is critical to successfully locate food, find refuge and avoid high mortality rates in these dynamic landscapes (Southwood, 1988). In temperate regions, habitat fragmentation is known to negatively affect natural enemies (Kruess and Tscharntke, 1994; Tscharntke and Kruess, 1999), especially specialists of higher trophic levels such as parasitoids (Chaplin-Kramer et al., 2011; Rand et al., 2012). However, Fahrig (2003) showed in a review that the responses of habitat fragmentation on agro-ecosystems species were nearly as positive as negative. In the present study, most of the functional groups including herbivores, parasitoids and detritivores/tourists responded negatively to the fragmentation of the rice habitat (Chapter 4). These findings suggest that herbivores do not benefit from the proximity of complementary resources found in neighbouring rice fields and are more likely to show a positive density-area relationship in the rice habitat (Chapter 4).

Similarly, parasitoids benefited more from the diversity of crop types found at the ecotone between crop and non-crop habitats (Chapter 5), and from the structural connectivity of the rice bunds (Chapter 4) than from the fragmentation of the rice habitat. Parasitoids require different resources such as nectar during their life cycle and increased configurational heterogeneity may enhance their presence by facilitating their movement in the rice habitat via landscape complementation (Dunning et al., 1992; Tscharntke et al., 2005; Fahrig et al., 2011). If the amount of rice is held constant, the fragmentation of the rice habitat results in the subdivision of several patches of rice that only differ in size and shape. Consequently, this implies smaller distances between patches, which reduces habitat isolation and can facilitate immigration of low mobility species (Fahrig, 2003). In asynchronous rice fields, the proximity and diversity of crops at different growth stages of the plant should provide predators with a constant source of food; and when rice fields are more interspersed with each other (increased structural connectivity of the bunds), their dispersal may be enhanced. Indeed, fields at different stages of the rice plant harbour different communities of arthropods (Wilby et al., 2006; Schoenly et al., 2010). Predators and to a further extent species with low dispersal mobility were favoured in highly fragmented rice habitats (Chapter 5). Additionally, increased connectivity of the rice bunds supported a higher number of predator species (Chapter 4). These findings suggest that predators likely benefit from easy access to neighbouring crops at different stages of the rice plant via landscape supplementation, resulting in faster recolonization rates (Dunning et al., 1992; Fahrig et al., 2015). For example, Settle et al. (1996) suggested that detritivores constitute an alternative source of food for generalist predators when herbivore abundance remains low during the early stages of the rice plant in Indonesia.

Importantly, contrasting responses of predators to the fragmentation of the rice habitat and the shape complexity of the rice patches were found in Chapter 4 and 5. While the results of Chapter 4 suggested that highly mobile predators would benefit from the fragmentation of the rice habitat, the opposite was observed in Chapter 5 where predators with low dispersal ability were actually favoured. Similarly, in contrast to the findings of Chapter 4, rice fields of irregular shapes supported more predators than rice fields of regular shapes in Chapter 5. The disparity of these results could be explained by the different measures of biodiversity (taxonomic vs functional; see **6.3.1.**) along with different statistical methods to test the effects of landscape heterogeneity on the arthropods. Additionally, it could be the influence of other factors than landscape heterogeneity, such as regional-scale effects (i.e. elevation, management practices, etc.), which were indirectly accounted in the analyses in Chapter 4. Nevertheless, the findings of Chapters 3, 4, and 5 highly suggest that other factors than landscape heterogeneity play a role in shaping rice-arthropod communities.

### 6.1.3 Additional drivers at play

In addition to landscape heterogeneity, rice arthropods responded to regional-scale effects (Chapter 3 and 4) and predators displayed a strong numerical response to prey density (Chapter 4).

In Chapter 3, regional-scale effects were measured by using elevation as a surrogate for climate, environmental conditions and land management factors operating at a regional scale. Firstly, regional-scale effects had direct effects on the rice-arthropod communities. At high elevation, arthropod abundances decreased, similarly as in Schoenly et al. (1996). In addition, elevation was shown to be a limiting factor for the fitness of *N.lugens*, as previously stated by Settele (1992). With the absence of its main competitor (*N.lugens*), the white-backed planthopper (*S.furcifera*) thrives at high altitude (Chapter 3). Secondly, regional-scale effects had indirect effects on the rice-arthropod communities. When landscape heterogeneity was measured at a fine-scale (100 m), the regional-scale effects better explained the composition of the arthropod assemblages unique to each region (Chapter 3). The variability of the regional-scale effects was high among regions but low within regions, suggesting that these effects were indeed specific to each region. Each region in the study systems differed by its cultural identity, landscape structural diversity, and management practices (mechanization and chemical inputs) (see 2.1.1.). In Chapter 1, I highlighted the negative impacts of the overuse of chemical inputs on the rice arthropod community. The lowland regions (PH_1 and PH_2) are generally associated with increased use of chemical inputs (i.e. pesticides, fertilizers, etc) and mechanization in rice farming systems. On the other hand, the mountainous region (PH_3) lacks any form of mechanization and farmers still rely on traditional rice varieties and less pesticide applications. In addition, the access to water to irrigate the crops greatly differs from one region to another (rainfed vs irrigated systems). In other words, it is most likely a combination of factors specific to each region rather than elevation alone that explained the composition of rice arthropod assemblages in Chapter 3. This further suggests that regional-scale effects cannot be fully disentangled from landscape heterogeneity in the present thesis (Chapter 3, 4 and 5).

While some regional-scale effects have the potential to disrupt the food web structure of rice arthropods, trophic interactions are the key to maintain it (Chapter 4). More specifically, the findings of Chapter 4 indicated that predator populations were largely driven by the availability of prey such as herbivores species and detritivores, while also poorly responding to landscape heterogeneity. This suggests that the availability of prey in the rice fields rather than landscape heterogeneity better explained the abundance of predators in Chapter 4. However, with regard to the results of Chapter 5, the density dependence relationships further supported the hypothesis that predators also benefit from increasing configurational heterogeneity via landscape supplementation (see **6.1.2.**). Most of the predators identified in the current thesis are generalist predators such as spiders or aquatic predators that can feed on multiple species. Therefore, the presence of substitutable resources in the neighbouring rice fields such as detritivores (Settle et al., 1996) can provide predators with a continuous source of food and their movement is facilitated by high configurational heterogeneity.

## 6.2 Recommendations for the management of rice agro-ecosystems at the landscape level

One of the main objectives of the LEGATO project was to find solutions to achieve sustainable rice production in Southeast Asia. While landscape ecology approaches are still rare in rice agro-ecosystems, the present thesis can provide an early insight into how the rice agro-ecosystems can be spatially managed to enhance natural biological control at the landscape level. The key for a successful natural biological control story is to achieve the two following objectives: keeping herbivores populations at low density and enhancing natural enemy populations. The findings of this thesis indicated that the composition of the non-crop habitats and the spatial arrangement of the rice habitat could be determinant for the enhancement of biological control. To minimize the presence of herbivores, the landscape surrounding the rice fields should be highly diverse and rice fields should be managed in small and numerous patches across the landscape. Therefore, asynchronous cropping is recommended when possible, as fragmentation of the rice habitat can support predator populations via landscape supplementation. The bunds surrounding the rice fields can facilitate the movement of natural enemies (i.e. parasitoids), and thus should be appropriately managed to maximize their connectivity. Ecological engineering approaches, such as increasing the floral diversity of the rice bunds, can provide additional resources to natural enemies such as shelter and food (Gurr et al., 2016); hence their application in the fields is recommended. However, the fragmentation of the rice habitat can select against different natural enemy groups and emphasis should be put into finding the optimal spatial arrangement of the rice habitat that encourages the simultaneous presence of multiple natural enemies (Chapter 5).

Additionally, habitat manipulation should be carefully monitored by keeping the farmers' best interest at heart. Rice habitats are managed by a community of smallholder farmers where spatial structures and irrigation systems are often shared; hence the margin for habitat manipulation is often limited and its adoption requires a community approach. For example, asynchronous cropping may not be feasible in areas where access to water is limited. In addition, the fragmentation of the rice habitat can lead to mechanization constraints, which ultimately led to the increase in production costs in Japan (Kawasaki, 2010). At the farm and local scale, ecological engineering approaches in rice can provide farmers with supplementary crops like sesame or vegetables which may increase the farmer's income. In a recent study, Gurr et al. (2016) have demonstrated that the increased rice yields and lesser use of pesticides resulting from ecological engineering applications outweighed the costs of establishing and harvesting other crops or plants from the rice bunds. However, it may prove difficult to convince the farmers at the community level to implement these approaches on a larger scale in comparison to the easy access of pesticide use in the Philippines.

## 6.3 Limitations and perspectives

To my knowledge, the findings of this thesis were the first to quantify the effects of landscape heterogeneity on arthropods in rice agro-ecosystems. As a result, this thesis acts as a pioneer for further research, thus providing useful initial information for the enhancement of natural biological control at the landscape level. Nevertheless, the present thesis was not exempt of limitations and further research is still needed to fully explore the complex interactions between pests, natural enemies, and landscape heterogeneity in rice agro-ecosystems.

### 6.3.1 Decomposing arthropod biodiversity: Taxonomic vs functional diversity

What is biodiversity? How is it distributed across biomes? And how do we measure it? Yet simple, these questions have long been the major focus of ecologists (Sutherland et al., 2013). Biodiversity can be defined as the variety of life forms, and thus, it has traditionally been measured with taxonomic indices such as abundance, number of species and species diversity (Ricklefs, 2003). In Chapter 3, taxonomic diversity was used to describe the rice-arthropod community and to identify the unique arthropod assemblages across the three studied regions.

However, different species contribute differently to the ecosystem functioning, according to the characteristics and interactions of different environments (Tilman, 1999; Luck et al., 2009). As a first attempt to explore different components of biodiversity, species sharing similar resources were categorized into functional groups (Root, 1967). For example, the functional group "predator", as described in the current thesis and previous studies (Heong et al., 1991; Heong et al., 1992; Settle et al., 1996), included many different species of arthropods such as spiders, ladybugs, aquatic insects, as well as hemipteran and heteropteran insects. Although, these predatory arthropods share the same diet, they greatly differ in regard to their other functional traits, from their body size to their dispersal ability. Studies focusing on the responses of specific functional traits to environmental change have received increased attention in recent years (Kleyer et al., 2012; Duflot et al., 2014; Gàmez-Virués et al., 2015). Functional diversity not only complements taxonomic diversity (Petchey and Gaston 2002), it may also be one of the best predictors of ecosystem functioning (Gagic et al., 2015). In Chapter 5, the multiple-traits approach helped differentiating the effects of landscape heterogeneity on herbivore and predator species that differed in their functional traits (e.g. dispersal ability). Therefore, by measuring different aspects of arthropod biodiversity at multiple scales, the present thesis highlighted the differences in arthropod responses to landscape heterogeneity when using both taxonomic and functional diversities. However, trait information for arthropods is relatively scarce, especially in rice agro-ecosystems; hence trait databases need to be more developed in the future. Additionally, while dispersal ability was determined by wing morphology of the species, it was yet quantified in terms of arthropod abundance in Chapter 5, rather than individual movement behaviour. There is a need for more experiments in rice agro-ecosystems that quantify emigration and immigration rates of herbivores and natural enemies to improve the understanding of arthropod movement among rice patches.

Ultimately, there is no one simple measure of biodiversity. Biodiversity is a multi-faceted concept that encompasses not only taxonomic and functional diversity, but also phylogenetic and genetic diversity (Naeem et al., 2016, Fournier et al., 2017). Phylogenetic diversity, for example, can provide information to the evolutionary relationships among species and can be related to ecosystem functioning and ecosystem services (Winter et al., 2013). Since taxonomic, functional and phylogenetic diversities can have different responses to environmental conditions (Fournier et al., 2017 but see results from Chapter 4 and 5), future research will need to consider these different components of biodiversity altogether to fully understand the patterns of biodiversity in rice agro-ecosystems (Naeem et al., 2016; Fournier et al., 2017).

Finally, it is important to note that the findings of the present thesis were the results of a single year of data collection and reflected the dynamic of rice-arthropods during the dry cropping season only. While data was available for two consecutive years in the low-lands, the mountainous region was visited just once during 2014. Due to the uniqueness of Ifugao (PH_3) rice terraces, the research questions embedded in the context of this project rather focused on a valuable comparison of the three study regions than on temporal variability. The configuration of the rice agro-ecosystems changes in time and space through the years, and thus, research focusing on the temporal changes should also take into account the spatial variation of the rice crops (see 6.3.2. for more details).

### 6.3.2 Measuring landscape heterogeneity at multiple scales

The multi-level approach to measure landscape heterogeneity in this thesis highlighted the need to use modern tools (e.g. GIS software and remote sensing data) to best describe landscape heterogeneity in rice agro-ecosystems. By comparing low and high heterogeneity sites in Chapter 3, landscape heterogeneity was described via visual assessment and its effects on the rice-arthropod community were merely discernible. In the following chapters (4 and 5), the use of landscape metrics to quantify both the composition and configuration of the landscape has proven to be an effective method in assessing the influence of landscape heterogeneity on rice-arthropods. Additionally, landscape heterogeneity was measured at multiple spatial scales to identify the scale of effect of the landscape on arthropods.

The scale of effect can be described as the spatial scale to which landscape heterogeneity best predicts species responses (Jackson and Fahrig, 2012). In Chapter 4, the different arthropod species responded to landscape heterogeneity at different spatial scales, most likely reflecting their dispersal abilities (Steffan-Dewenter et al., 2001). These findings provided useful information as to which resources each species requires to be managed to increase their presence in the landscape. However, some of the results from Chapter 4 and 5 may depend on the particular spatial scale selected for the analysis. This thesis was conducted within the interdisciplinary and transdisciplinary project LEGATO where the study sites were selected according to their potential transferability to other regions (e.g. Vietnam). The mean distance between two core sites within each pair being ~ 369 m, the largest spatial scale of 300 m radii was selected in order to best avoid overlapping landscape buffers and violation of spatial independence. For example, it is possible that the effects of landscape heterogeneity on the diversity of predators would be noticeable at spatial scales larger than the ones selected in the present thesis. Future research should test the responses of rice arthropods at larger scales than 300 m radii.

While the main objective of this thesis was to identify the potential benefits of non-crop habitats and configurational heterogeneity on rice arthropods, the findings of Chapter 4 and 5 suggested that the composition of the rice habitat itself was just as important in shaping rice arthropod communities. In both Chapters 4 and 5, landscape diversity was calculated at the landscape level with all the land cover categories, with rice being identified as a single land use category. However, rice agro-ecosystems are a dynamic mosaic of rice fields at different temporal stages that vary in space and time. As the rice plant grows, the rice arthropod community changes as well. For example, the community is dominated by detritivores species during the seedling stage, whereas predator species become more abundant at the tillering stage and herbivores at the booting/flowering stage (Wilby et al., 2006). These effects were accounted in this study via the sampling of arthropods at the same stage of the plant (50 DAT). However, neighbouring fields were not controlled and differed in their growth stages. In asynchronous cropping landscapes, different rice fields at different growth stages could benefit natural enemies via landscape supplementation and/or complementation (Chapters 4 and 5). In addition, little is known about the movement behaviour of rice arthropods among neighbouring rice patches and their colonization rates. Thus, rice fields at different growth stages may have different effects on arthropods based on their spatial arrangement. Consequently, the rice habitat is not a homogeneous land use category as described in this thesis, but a heterogeneous landscape of complex rice patches at different growth stages. Spatial heterogeneity can be described as the configuration or spatial arrangement of the rice crop, while temporal heterogeneity can be defined by the composition of the rice crop (stage of the growth plant, crop rotation, ratoon crop, and fallow period). Further research is in dire need to test the effects of spatial and temporal heterogeneity of rice habitats on the arthropod community.

### 6.3.3 Land use intensity and local management

The findings of this thesis have demonstrated the importance of landscape composition and configuration in shaping the rice arthropod communities. However, land-use intensity (i.e. chemical inputs, mechanization, and local management practices) is also considered as an important driver of biodiversity (Fahrig, 2013; Gerstner et al., 2014; Seppelt et al., 2016). More specifically, the overuse of pesticides has a negative impact on the rice arthropod communities (see 1.2.). In their conceptual framework, Seppelt et al. (2016) suggested that increased compositional and configurational heterogeneity may result in land-use intensification being less effective for crop production. To fully understand the effects of land-use on the biodiversity of rice agro-ecosystems, future research should focus on the multiple aspects of land-use, including land-use intensity.

However, quantifying or measuring pesticide applications in the Philippines has proven to be difficult. Instead of selecting the proper pesticide, Filipino farmers usually resort to spray "cocktails of pesticides" that combine multiple pesticides altogether (insecticide, herbicide, fungicide, etc.) (Heong, pers.comm.). As a result, it is more difficult to assess how frequently and which active ingredients farmers are using in their fields. In Northern Vietnam, Sattler et al. (2018) were however able to evaluate pesticide use by collecting pesticide packages in the field. Additionally, farmers that were interviewed within the LEGATO project gave contrasting responses regarding pesticide use. Moreover, drift from sprayed to non-sprayed fields can happen during pesticide application, but the general effects are still poorly understood (Horgan, pers.comm.). With the resurgence of pesticides as the primary tool to control rice pests, better information and education are more than ever necessary in the Philippines to reduce pesticide use.

In Chapter 5, I hypothesized that a combination of landscape metrics (landscape diversity, number of rice patches, and core area index) could help identify patterns of land-use intensity in the Philippines. Indeed, the mountainous region of PH_3 (no mechanization and low chemical input) is characterized by highly heterogeneous sites subdivided in multiple smaller rice patches of irregular shape. On the other hand, the lowlands regions of PH_1 and PH_2 (low mechanization and high chemical input) are characterized by homogeneous landscapes comprised of larger but fewer rice patches of regular shape. However, my raw data cannot directly support the hypothesis proposed above. Nevertheless, the findings of the present thesis suggest that land-use intensity is likely confounded or in interaction with the effects of landscape heterogeneity.

## 6.4 Conclusion

The importance of landscape heterogeneity in shaping the rice arthropod communities has been established in this thesis. The availability of non-crop habitats at the ecotone of the rice habitat and the spatial arrangement of the rice habitat can benefit natural enemies and reduce pest densities. The rice bunds provide an interesting prospect for ecological engineering applications as they can facilitate the movement of natural enemies and offer them additional shelter and resources. In addition, the spatial and temporal heterogeneity of the rice habitat may benefit generalist predators via landscape supplementation.

The methods that have been used in this thesis have showed the importance of adopting modern tools to quantify the landscape heterogeneity of rice agro-ecosystems. The multi-level approach in describing the rice arthropod biodiversity supports the idea that functional diversity complements taxonomic diversity in studying arthropod diversity in rice agro-ecosystems.

Finally, this thesis acts as a pioneer for further landscape ecology approaches in rice agro-ecosystems, and its findings provide useful information for the enhancement of natural biological control at the landscape level.

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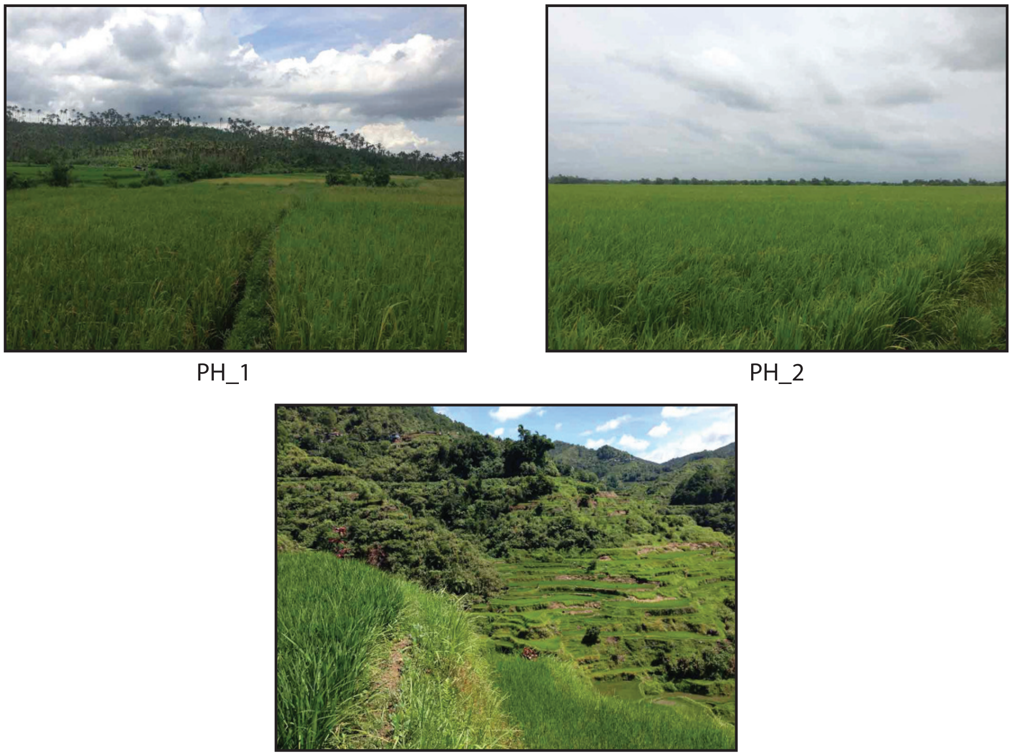
# Appendices

## Appendix A



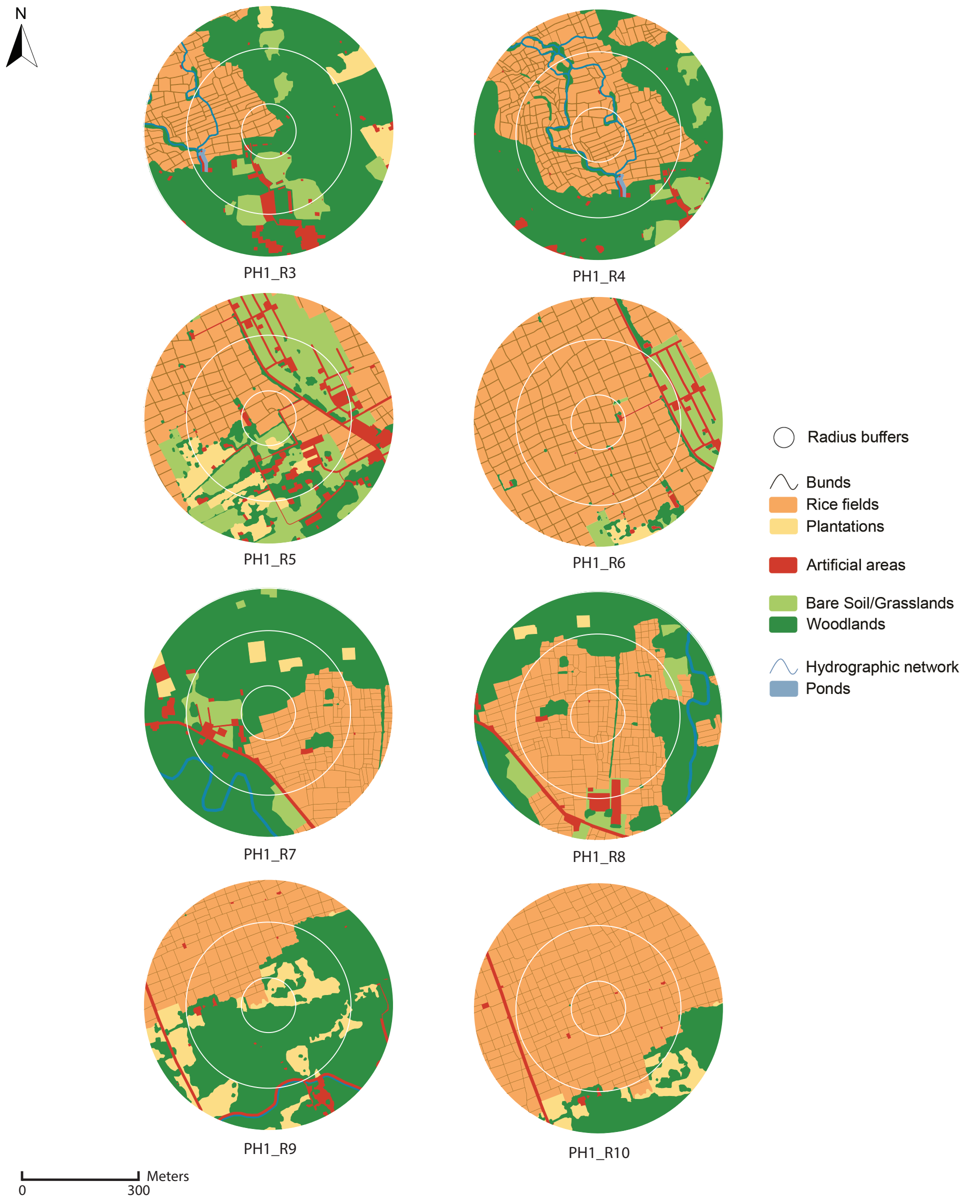
PH_1

PH_2

PH_3

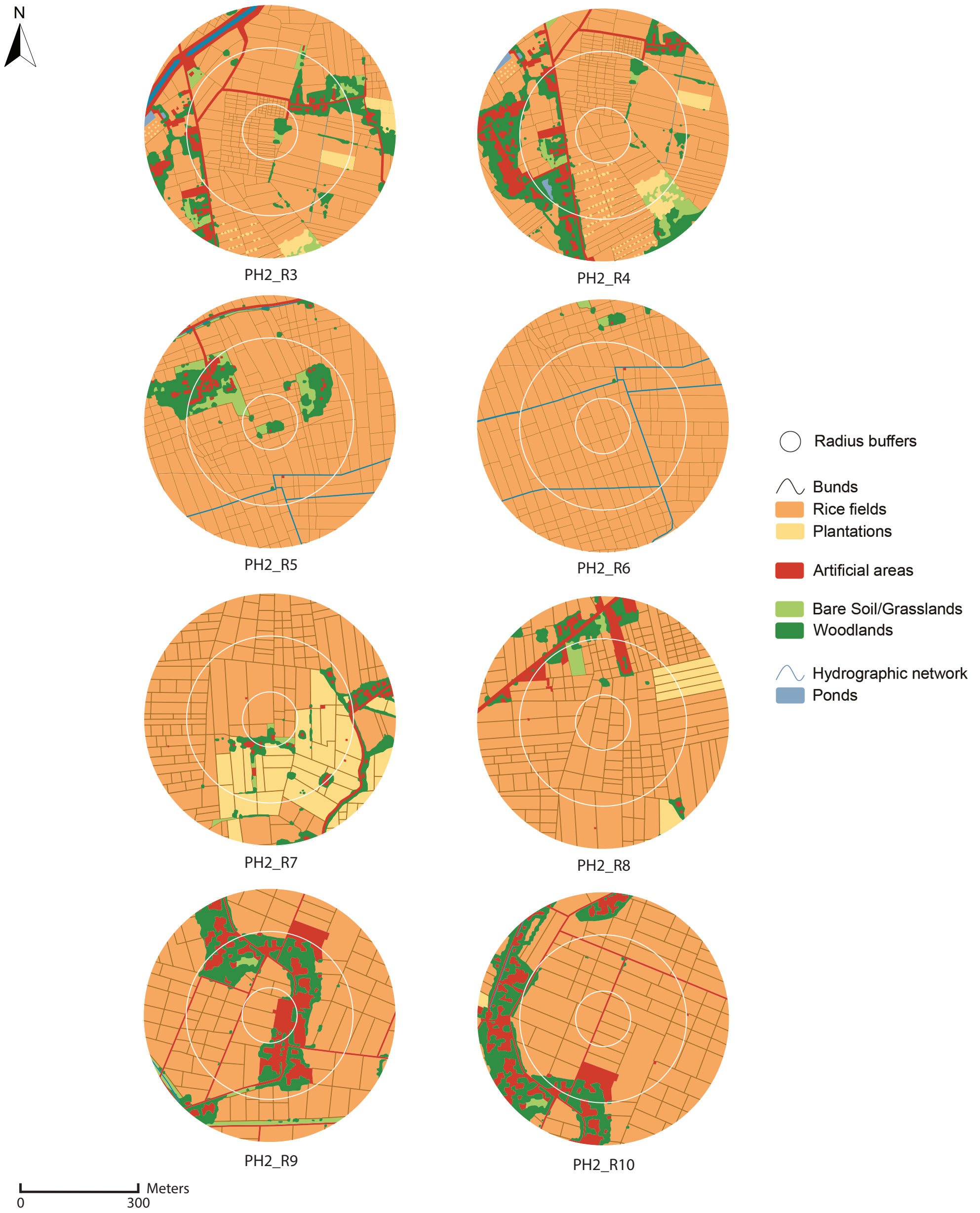
Typical rice landscape of each study region.

## Appendix B



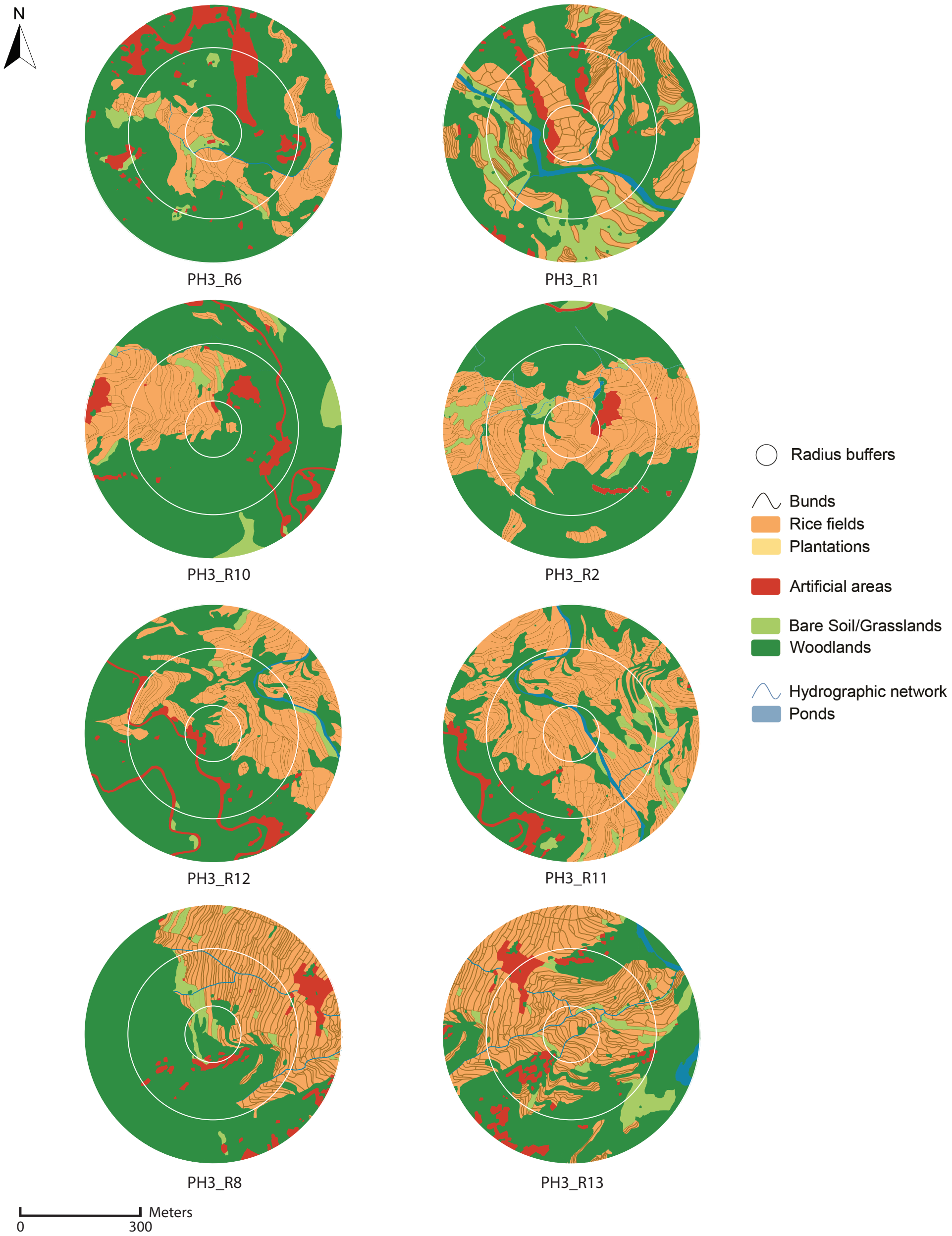
Remaining digitized maps for the region PH_1. High heterogeneity sites are represented on the left. Low heterogeneity sites (associated paired to high heterogeneity sites) are represented on the right.

## Appendix C



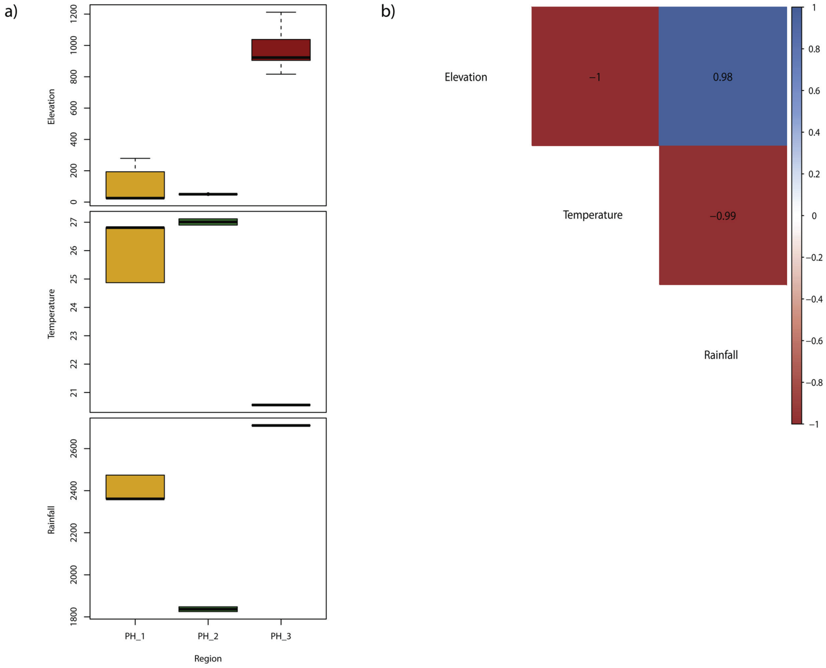
Remaining digitized maps for the region PH_2. High heterogeneity sites are represented on the left. Low heterogeneity sites (associated paired to high heterogeneity sites) are represented on the right.

## Appendix D



Remaining digitized maps for the region PH_3. High heterogeneity sites are represented on the left. Low heterogeneity sites (associated paired to high heterogeneity sites) are represented on the right.

## Appendix E



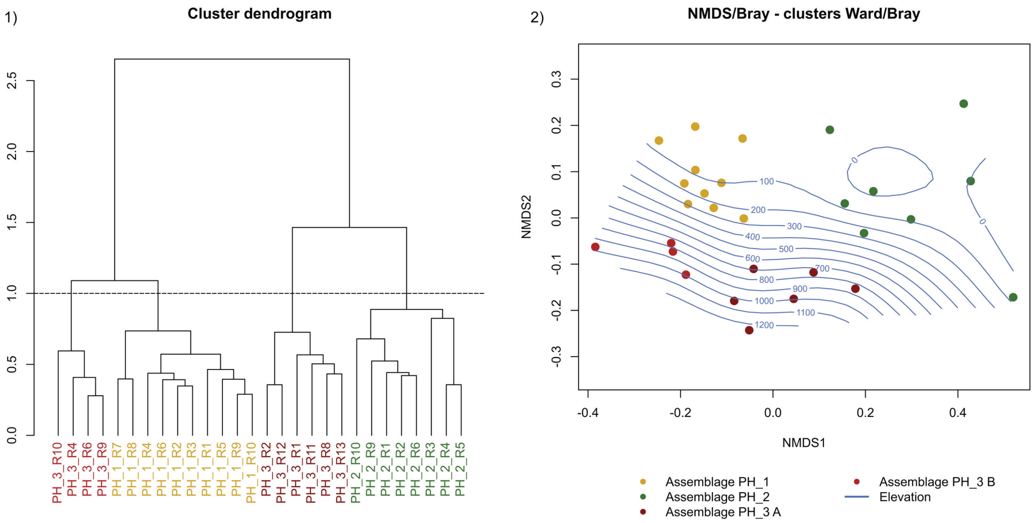
a) Box plots representing the variability of elevation (m), temperature (°C) and rainfall (m) across the three regions. b) Results of the Pearson correlation test used for multicollinearity among the environmental variables (All results showed $P > 0.001$).

## Appendix F

Name, family, order, guild (functional group), abundance and contribution of the 213 morphospecies identified in the three regions for each sampling method. Guild represents the four functional groups with 1: Herbivores; 2: Predators; 3: Parasitoids; 4: Detritivores/Tourists. Avg. abundances represent the average abundance of each morphospecies in each region. Contribution represents the contribution of each morphospecies in each region in percent. Total abundance represents the total mean abundance of each species across the three regions. Please find the appendix online at the following address:

https://figshare.com/articles/AppendixA_xls/4004712

# Appendix G



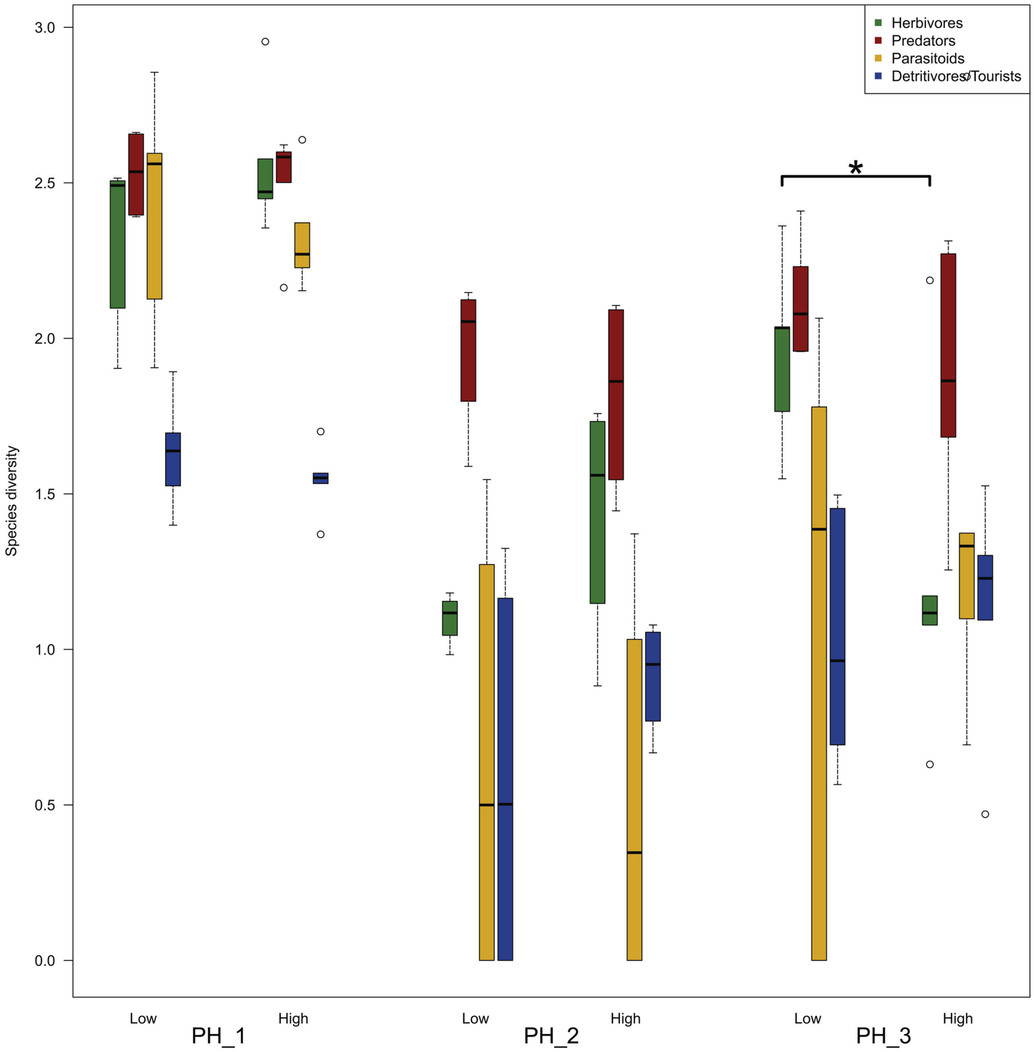
1) Ward's hierarchical cluster analysis based on Bray-Curtis dissimilarity matrix using square-root transformed arthropod mean abundance data of 28 core sites (data shown for the sweep-net samples). The cluster analysis identified four distinct assemblages (distinguished by color), each associated with one region (except for PH_3 where two assemblages were found). Core sites are abbreviated using the following nomenclature: PH represents the region; R represents the core site (i.e. PH_1_R2: Core site number 2 located in the region PH_1). 2) Non-metric multidimensional scaling (NMDS) analysis of the Bray-Curtis dissimilarity matrix (data shown for the sweep-net samples). The distance between sites indicates similarity of the arthropod community-the closer, the more similar. The variable that best explained the assemblage structure (i.e. elevation) is shown as surface fitting.

## Appendix H

| | Blow vac | | | | Sweep net | | | |
|---|---|---|---|---|---|---|---|---|
| | **ANOVA Elevation** | | **Paired test Landscape Heterogeneity** | | **ANOVA Elevation** | | **Paired test Landscape Heterogeneity** | |
| **Morphospecies** | *t* | *p* | *Region* | *p* | *t* | *p* | *Region* | *p* |
| Nephottetix spp | -3.175 | 0.00395 | | | -2.424 | 0.0229 | | |
| Sogatella furcifera | 2.299 | 0.0362 | | | 3.519 | 0.00168 | | |
| Nilaparvata lugens | -3.872 | 0.000687 | | | | | | |
| Linyphiidae | -2.562 | 0.0168 | | | | | | |
| Lycosidae | -3.727 | 0.000995 | | | -2.428 | 0.022716 | | |
| Tetragnathiidae | | | | | | | | |
| Cyrtorhinus lividipennis | 2.595 | 0.0156 | | | 3.944 | 0.000571 | | |
| Micraspis spp | | | | | -2.561 | 0.0168 | | |
| Microvelia atrolineata | | | PH_2 Low | 0.02 | | | | |
| Formicidae | | | | | | | | |
| Gonatocerus spp | | | | | | | | |
| Tetrastichus spp | | | | | | | | |
| Trichogramma spp | -2.256 | 0.0331 | | | | | | |
| Oligosita spp | | | PH_1 High | 0.03 | | | | |
| Diptera others | | | | | | | | |
| Chironomidae | -2.312 | 0.00293 | | | | | | |

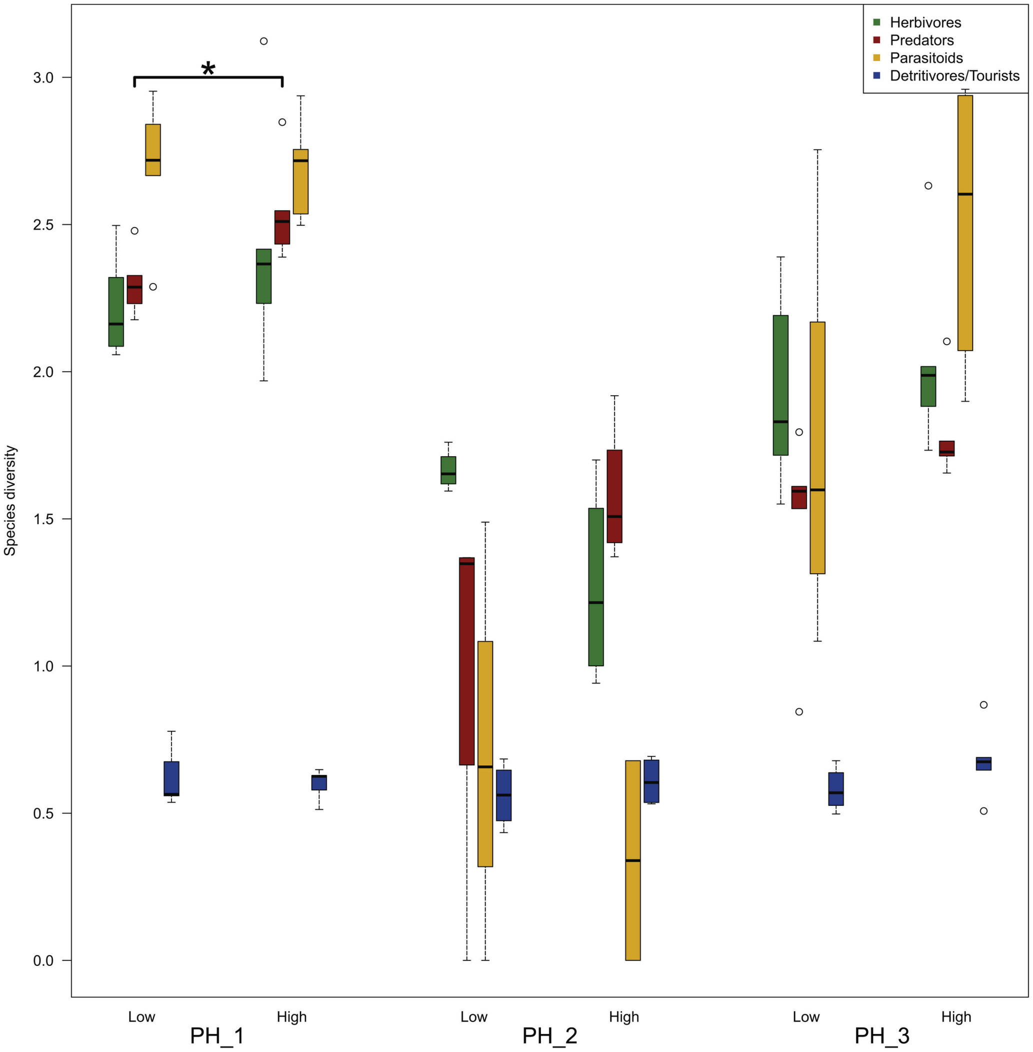
Summary of the one-way analysis of variance (ANOVA) testing the effects of elevation and fine-scale landscape heterogeneity on the 16 morphospecies that contributed most to the similarities within each arthropod assemblage for both blow-vac and sweep net samples (only significant results are shown), and results of the paired tests (Student's t-test when applicable and Mann Whitney test) testing the effect of fine-scale landscape heterogeneity within each region for each morphospecies in blow-vac and sweep net samples (only significant results are shown).

## Appendix I



Box-plots of the species diversity of functional groups for low heterogeneity sites ("Low") and high heterogeneity sites ("High") across the three regions (data derived from the blow-vac). Boxes show the median, 25th and 75th percentiles, maximum and minimum observations. Significant differences ($P < 0.05$) between low and high heterogeneity habitats are indicated by asterisks above and between boxes.

## Appendix J



Box-plots of the species diversity of functional groups for low heterogeneity sites ("Low") and high heterogeneity sites ("High") across the three regions (data derived from the sweep net). Boxes show the median, 25th and 75th percentiles, maximum and minimum observations. Significant differences ($P < 0.05$) between low and high heterogeneity habitats are indicated by asterisks above and between boxes.

# Appendix K

| Morphospecies | Family | Order | Code | Body (mm) | Dispersal | Guild | Specialization | Stratum |
|---|---|---|---|---|---|---|---|---|
| Acanthalobus sp. 1 | Tetrigidae | Orthoptera | ACANTH | 11.7 | Macropterous | Herbivores | Generalist | Canopy |
| Aeoloderma brachmana | Elateridae | Coleoptera | AEOBRA | 7 | Macropterous | Herbivores | Generalist | Base |
| Aleurocybotus spp. | Aleyrodidae | Hemiptera | ALEURO | 2.5 | Macropterous | Herbivores | Generalist | Canopy |
| Anagrus spp. | Mymaridae | Hymenoptera | ANAGRU | 0.7 | Macropterous | Parasitoids | Specialist | Canopy |
| Anaxipha longipennis | Gryllidae | Orthoptera | ANALON | 13.1 | Brachypterous | Predators | Generalist | Canopy |
| Anisops sp. | Notonectidae | Heteroptera | ANISOP | 5.3 | Brachypterous | Predators | Generalist | Water |
| Aphids spp. | Aphididae | Homoptera | APHIDS | 2 | Brachypterous | Herbivores | Generalist | Base |
| Atypena formasana | Linyphiidae | Araneae | ATYFOR | 2.55 | Apterous | Predators | Generalist | Base |
| Ceraphon spp. | Scelionidae | Hymenoptera | CERAPH | 1.5 | Macropterous | Parasitoids | Specialist | Canopy |
| Chaetocnema spp. | Chrysomelidae | Coleoptera | CHAETO | 2 | Macropterous | Herbivores | Generalist | Canopy |
| Chironimid spp. | Chironomidae | Diptera | CHIRON | 2.5 | Macropterous | Detritivores | Generalist | Canopy |
| Cicadulina bipunctata | Cicadellidae | Homoptera | CICBIP | 2.65 | Brachypterous | Herbivores | Generalist | Canopy |
| Clubionid spp. | Clubionidae | Araneae | CLUBIO | 5 | Apterous | Predators | Generalist | Canopy |
| Coenagrionoid spp. | Coenagrionoidea | Odonata | COENAG | 25 | Macropterous | Predators | Generalist | Canopy |
| Cofana spectra | Cicadellidae | Homoptera | COFSPE | 9.5 | Brachypterous | Herbivores | Specialist | Canopy |
| Conocephalus longipennis | Tettigoniidae | Orthoptera | CONLON | 14 | Macropterous | Herbivores | Generalist | Canopy |
| Cotesia spp. | Braconidae | Hymenoptera | COTESI | 3.5 | Macropterous | Parasitoids | Specialist | Canopy |
| Cyrtorhinus lividipennis | Miridae | Heteroptera | CYRLIV | 2.75 | Macropterous | Predators | Specialist | Canopy |
| Drynid sp. 1 | Dryinidae | Hymenoptera | DRYNID | 3 | Apterous | Parasitoids | Specialist | Canopy |
| Diplonychus sp. 1 | Belostomidae | Heteroptera | DYPLON | 15 | Brachypterous | Predators | Generalist | Water |
| Elasmus spp. | Elasmidae | Hymenoptera | ELASMI | 1.2 | Macropterous | Parasitoids | Specialist | Canopy |
| Empoascanara maculifrons | Cicadellidae | Homoptera | EMPMAC | 3.5 | Brachypterous | Herbivores | Specialist | Canopy |
| Entomobryid spp. | Entomobryidae | Collembola | ENTOMO | 1 | Apterous | Detritivores | Generalist | Base |
| Formicid spp. | Formicidae | Hymenoptera | FORMAC | 3.3 | Apterous | Predators | Generalist | Base |
| Galerucinae Aulacophora | Chrysomelidae | Coleoptera | GALAUL | 8 | Macropterous | Herbivores | Generalist | Canopy |
| Gonatocerus spp. | Mymaridae | Hymenoptera | GONATO | 1.8 | Macropterous | Parasitoids | Specialist | Canopy |
| Gryon nixoni | Scelionidae | Hymenoptera | GRYNIX | 1.6 | Macropterous | Parasitoids | Specialist | Canopy |
| Helocares sp. 1 | Hydrophilidae | Coleoptera | HELOCA | 2.9 | Macropterous | Herbivores | Generalist | Water |
| Hemiptarsenus sp. | Eulophidae | Hymenoptera | HEMIPT | 2 | Macropterous | Parasitoids | Specialist | Canopy |
| Hydrometra lineata | Hydrometridae | Heteroptera | HYDLIN | 13.3 | Brachypterous | Predators | Generalist | Water |
| Idris sp. | Scelionidae | Hymenoptera | IDRISS | 1.5 | Macropterous | Parasitoids | Specialist | Canopy |
| Isotomid spp. | Isotomidae | Collembola | ISOTOM | 1 | Apterous | Detritivores | Generalist | Base |
| Laccophilus spp. | Dytiscidae | Coleoptera | LACCOP | 3.5 | Macropterous | Predators | Generalist | Water |
| Limnogonus spp. | Gerridae | Heteroptera | LIMNOG | 10 | Brachypterous | Predators | Generalist | Water |
| Mesovelia vittigera | Mesoveliidae | Heteroptera | MESVIT | 2.8 | Brachypterous | Predators | Generalist | Water |
| Microvelia douglasi atrolineata | Veliidae | Heteroptera | MICDOU | 2.2 | Brachypterous | Predators | Generalist | Water |
| Micronecta quadristrigata | Corixidae | Heteroptera | MICQUA | 2.55 | Apterous | Predators | Generalist | Water |
| Micraspis spp. | Coccinellidae | Coleoptera | MICRAS | 3.5 | Macropterous | Predators | Generalist | Canopy |
| Monolepta spp. | Chrysomelidae | Coleoptera | MONOL | 3 | Macropterous | Herbivores | Generalist | Canopy |
| Mymar taprobanicum | Mymaridae | Hymenoptera | MYMTAP | 0.7 | Macropterous | Parasitoids | Specialist | Canopy |
| Nephotettix spp. | Cicadellidae | Homoptera | NEPHOT | 4 | Brachypterous | Herbivores | Specialist | Canopy |
| Nephotettix nigropictus | Cicadellidae | Homoptera | NEPNIG | 3.2 | Brachypterous | Herbivores | Specialist | Canopy |
| Nilaparvata lugens | Delphacidae | Homoptera | NILLUG | 4 | Brachypterous | Herbivores | Specialist | Base |
| Nisia atrovenosa | Meenoplidae | Homoptera | NISATR | 2 | Brachypterous | Herbivores | Generalist | Canopy |
| Oligosita spp. | Trichogrammatidae | Hymenoptera | OLIGOS | 0.5 | Macropterous | Parasitoids | Specialist | Canopy |
| Ophionea nigrofasciata | Carabidae | Coleoptera | OPHNIG | 7 | Macropterous | Predators | Generalist | Canopy |
| Opius barrioni | Braconidae | Hymenoptera | OPIBAR | 2.2 | Macropterous | Parasitoids | Specialist | Canopy |
| Orius tantillus | Anthocoridae | Homoptera | ORITAN | 2.5 | Macropterous | Predators | Generalist | Canopy |
| Oxya spp. | Acridoididea | Orthoptera | OXYASP | 25 | Macropterous | Herbivores | Generalist | Canopy |
| Oxyopes lineatipes | Oxyopidae | Araneae | OXYLIN | 8 | Apterous | Predators | Generalist | Canopy |
| Paederus fuscipes | Staphylinidae | Coleoptera | PAEFUS | 6.75 | Macropterous | Predators | Generalist | Base |
| Paraphylax sp. 2 | Braconidae | Hymenoptera | PARAPH | 1.3 | Macropterous | Parasitoids | Specialist | Canopy |
| Pardosa pseudoannulata | Lycosidae | Araneae | PARPSE | 9.95 | Apterous | Predators | Generalist | Base |
| Pediobus sp. 1 | Eulophidae | Hymenoptera | PEDIOB | 1.2 | Macropterous | Parasitoids | Specialist | Canopy |
| Phalacrinus sp. 1 | Phalacridae | Coleoptera | PHALAC | 2.7 | Macropterous | Detritivores | Generalist | Canopy |
| Platygasterid sp. 1 | Platygasteridae | Hymenoptera | PLATYG | 0.95 | Macropterous | Parasitoids | Specialist | Canopy |
| Recilia dorsalis | Cicadellidae | Homoptera | RECDOR | 3.75 | Brachypterous | Herbivores | Specialist | Canopy |
| Salticid spp. | Salticidae | Araneae | SALTIC | 4.88 | Apterous | Predators | Generalist | Canopy |
| Scotinophara spp. | Pentatomidae | Heteroptera | SCOTIN | 9 | Macropterous | Herbivores | Generalist | Canopy |
| Sminthurid spp. | Sminthuridae | Collembola | SMINTH | 1 | Apterous | Detritivores | Generalist | Base |
| Sogatella furcifera | Delphacidae | Homoptera | SOGFUR | 3.75 | Brachypterous | Herbivores | Specialist | Base |
| Staphylinid sp. 1 | Staphylinidae | Coleoptera | STAPHY | 6.75 | Macropterous | Predators | Generalist | Base |
| Stenus sp | Staphylinidae | Coleoptera | STENUS | 3.73 | Macropterous | Predators | Generalist | Base |
| Copidosomopsis nacoleiae | Encyrtidae | Hymenoptera | TELENO | 1 | Macropterous | Parasitoids | Specialist | Canopy |
| Telenomus sp. 4 | Scelionidae | Hymenoptera | TELENO1 | 1.5 | Macropterous | Parasitoids | Specialist | Canopy |
| Tetragnathid spp. | Tetragnathidae | Araneae | TETRAG | 9.6 | Apterous | Predators | Generalist | Canopy |
| Tetrastichus sp. 1 | Eulophidae | Hymenoptera | TETRAS | 3 | Macropterous | Parasitoids | Specialist | Canopy |
| Theridiid spp. | Theridiidae | Araneae | THERID | 3.7 | Apterous | Predators | Generalist | Canopy |
| Thomisid spp. | Thomisidae | Araneae | THOMIS | 5.75 | Apterous | Predators | Generalist | Canopy |
| Haplothrips spp | Phlaeothripidae | Thysanoptera | THYSAN | 1.5 | Macropterous | Herbivores | Generalist | Canopy |
| Trichomalopsis apanteloctena | Pteromalidae | Hymenoptera | TRIAPA | 1.77 | Macropterous | Parasitoids | Specialist | Canopy |
| Trichogramma chilonis | Trichogrammatidae | Hymenoptera | TRICHI | 0.5 | Macropterous | Parasitoids | Specialist | Canopy |
| Trichogramma sp. 1 | Trichogrammatidae | Hymenoptera | TRICHO | 0.5 | Macropterous | Parasitoids | Specialist | Canopy |
| Trichogramma sp. 2 | Trichogrammatidae | Hymenoptera | TRICHO1 | 0.5 | Macropterous | Parasitoids | Specialist | Canopy |
| Tytthus chinensis | Miridae | Heteroptera | TYTCHI | 2.7 | Macropterous | Predators | Specialist | Canopy |

Morphospecies name, family, order, code and species traits of the 75 morphospecies identified in the three regions for Chapter 5. Body represents the mean body length in mm, dispersal represents the disperal ability, guild represents the functional group, specialization represents the niche breadth and stratum represents the favored vertical stratum of the morphospecies.

# Christophe **Dominik**

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## Summary

Practical experience in landscape ecology, agro-ecology and community ecology. 8+ years experience in geographical information systems (GIS) and statistical software (R). 1+ year experience in field work and identification of arthropods. 1+ year abroad work experience (Philippines). Education in Science specialized in Landscape Ecology. Strong interest in landscape ecology, functional ecology, agro-ecology, R and data visualization.

## Education

**Martin Luther University Halle-Wittenberg** *Halle, Germany*
Dr. rer. nat. *2019*

**Université de La Réunion** *Saint-Denis, Réunion Island*
Master of Science in Biodiversity and Tropical Ecosystems *2011*

**Université Henri-Poincaré (UHP Nancy-1)** *Nancy, France*
Bachelor of Science in Biology of Organisms and Populations *2009*

## Skills

**Softwares** R (proficient), ArcGIS 9/10, ArcView 3.1, Fragstats, MARK, Adobe CS5 (Photoshop, Illustrator), Markdown, GitHub, LateX (beginner).

**Statistics** Multiple linear regressions, ANOVA, LME, GLM/GLMM, dissimilarity matrices, RLQ, fourth-corner analyses (traits analyses).

**Sampling methods** Sweep-net, suction sampler (blow-vac), pitfall trap, color plate, exclusion nets.

**Fauna identification** European arthropods (knowledge varies depending on Order), tropical rice-arthropods (Philippines).

**Languages** French (Native), English (Highly proficient), German (Good command).

## Research Experience

**Helmholtz Centre for Environmental Research (UFZ)** *Halle, Germany*
Postdoctoral researcher | Department of Community Ecology *Jan. 2019 - now*

- Mapping, fieldwork, landscape ecology, pollination services

**Helmholtz Centre for Environmental Research (UFZ)** *Leipzig, Germany*
PhD student/Guest scientist | Supervisors: Pr. Dr. Ralf Seppelt and Dr. Tomáš Václavík *Jul. 2012 - Dec. 2018*

- Research topic: The effects of landscape heterogeneity on arthropod communities in rice agro-ecosystems.
- Mapping of 30 study sites using ArcGIS 10.
- Quantification of the landscape heterogeneity via calculation of landscape metrics (Fragstats).
- Use of multiple linear regression models, linear mixed effects models, dissimilarity matrices, RLQ method, fourth-corner analyses.

**International Rice Research Institute (IRRI)** *Los Baños Laguna, Philippines*
Guest scientist *Jun. 2013 - Sep. 2014*

- Sampling of rice-arthropods and identification of arthropods (∼ 80000 individuals) to morphospecies level (∼ 200 species).
- Experience in networking with local researchers and supervision of field work assistants in the mountainous region of the Philippines.

### Centre national de la recherche scientifique (CNRS)

*Nantes, France*

RESEARCH ASSISTANT *Mar. 2012 - Jun. 2012*

- Research topic: Influence of landscape structures of the salinas on terrestrial bird distribution of the Ré Island (Western France).
- Bird counts of common European passerine birds in salinas during a two weeks period.
- Mapping of the salinas located in Ré Island using ArcView 3.1 and calculation of landscape metrics (Fragstats).
- Multivariate analysis and multiple regressions used to test links between landscape metrics and bird distribution (dissimilarity matrices, hierarchical clustering).

### Centre national de la recherche scientifique (CNRS)

*Nantes, France*

UNDERGRADUATE RESEARCH STUDENT | SUPERVISOR: DR. LAURENT GODET | M.SC.2 THESIS GRADE: 16.67/20 RANK: 2/17 *Feb. 2011 - Jun. 2011*

- Research topic: Influence of landscape structures of the salinas on terrestrial bird distribution in the Guérande basin (NW France).
- Material/Methods and analysis similar to research experience in 2012.

### CIRAD

*Saint-Pierre, Réunion Island*

UNDERGRADUATE RESEARCH STUDENT | SUPERVISOR: DR. SERGE QUILICI | M.SC.1 THESIS GRADE: 15.73/20 RANK: 5/35 *Jan. 2010 - Jun. 2010*

- Research topic: Biology study of the sawfly *Cibdela janthina*: Food specificity and characterization of the different larval instars.
- Infestation of four plant species within the Rosacea family with 40 larvae of *C.janthina*.
- Daily survival monitoring and GLM analysis.

## Publications

Settele, J., Heong, K.L., Kühn, I., ..., **Dominik C.**, ..., Wiemers M. (2018). Rice Ecosystem Services in South-East Asia. *Paddy and Water Environment*, **16**: 211-214.
https://doi.org/10.1007/s10333-018-0656-9

**Dominik C.**, Seppelt R., Horgan, F.G., Settele J., & Václavík T. (2018). Landscape composition, configuration, and trophic interactions shape arthropod communities in rice agro-ecosystems. *Journal of Applied Ecology*, **55**: 2461-2472.
https://doi.org/10.1111/1365-2664.13226

**Dominik C.**, Seppelt, R., Horgan, F.G., Marquez, L., Settele, J., & Václavík, T. (2017). Regional-scale effects override the influence of fine-scale landscape heterogeneity on rice arthropod communities. *Agriculture, Ecosystems & Environment*, **246**: 269–278.
https://doi.org/10.1016/j.agee.2017.06.011

**Dominik C.**, Ménanteau L., Chadenas C., & Godet L. (2012). The influence of salina landscape structures on terrestrial bird distribution in the Guérande basin (Northwestern France). *Bird Study*, **59**: 483- 495.
https://doi.org/10.1080/00063657.2012.715279

## Conference presentations

### Ecological Society of Germany, Austria, and Switzerland (GfÖ) Annual Meeting

*Vienna, Austria*

DOMINIK, C., HORGAN, F., SETTELE, J., SEPPELT, R., VÁCLAVÍK, T. *Sep. 2018*

- Landscape composition, configuration, and trophic interactions shape arthropod communities in rice agro-ecosystems.

### Rice Ecosystem Services in South-East Asian Landscapes - LEGATO final conference

*Banaue, Philippines*

DOMINIK, C., HORGAN, F., SETTELE, J., SEPPELT, R., VÁCLAVÍK, T. *Aug. 2016*

- How regional environmental drivers and landscape complexity affect species composition in rice-dominated agroecosystems.

### Ecological Society of Germany, Austria, and Switzerland (GfÖ) Annual Meeting

*Göttingen, Germany*

DOMINIK, C., VÁCLAVÍK, T., HORGAN, F., SETTELE, J., SEPPELT, R. *Sep. 2015*

- Effects of landscape structures on rice agroecosystem biodiversity and biological control across the Philippines.

### Rice Ecosystem Services in South-East Asian Landscapes – a LEGATO conference

*Yogyakarta, Indonesia*

DOMINIK, C., VÁCLAVÍK, T., HORGAN, F., SETTELE, J., SEPPELT, R. *Mar. 2015*

- The effects of landscape heterogeneity on the biocontrol-production function in the rice dominated agroecosystems.

### Sustainable Land Management status conference

*Berlin, Germany*

DOMINIK, C., VÁCLAVÍK, T., HORGAN, F., SETTELE, J., SEPPELT, R. *Apr. 2013*

- The effects of landscape heterogeneity on the biocontrol-production function in the rice dominated agroecosystems.

### LEGATO: Ecological Engineering in Asian Rice Landscapes

*Hanoi, Vietnam*

DOMINIK, C., VÁCLAVÍK, T., HORGAN, F., SETTELE, J., SEPPELT, R. *Feb. 2013*

- The effects of landscape heterogeneity on the biocontrol-production function in the rice dominated agroecosystems.

# Selbstständigkeitserklürung / Declaration under Oath

Ich erkläre an Eides statt, dass ich diese Arbeit selbstständig und ohne fremde Hilfe verfasst, keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt und die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen als solche kenntlich gemacht habe.

I declare under penalty of perjury that this thesis is my own work entirely and has been written without any help from other people. I used only the sources mentioned and included all the citations correctly both in word or content.

Datum

Name