

Spider food webs: influence of cropping cycle and landscape heterogeneity in Philippine rice ecosystems

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*In nature's infinite book of secrecy
A little I can read.*

- William Shakespeare

Contents

Abstract	5
Zusammenfassung.....	7
Chapter 1: General introduction	10
Rice	10
A brief introduction to the importance of rice	10
Rice biology and cultivation	11
Rice – a diverse agro-ecosystem.....	14
Planthoppers, pesticides, problems.....	15
Spiders	16
A brief introduction to spiders.....	16
Spiders: ubiquitous generalist predators.....	17
Spiders in agro-ecosystems and their potential for biological control.....	19
Spiders in rice-paddy ecosystems	21
Research objectives and thesis outline.....	22
References	24
Chapter 2: Spiders in rice-paddy ecosystems shift from aquatic to terrestrial prey and use carbon pools of different origin	31
Abstract.....	32
Introduction.....	33
Materials and methods.....	35
Results.....	39
Discussion	49
References	57
Chapter 3: Variation in the diet of spiders in rice paddy ecosystems of different landscape complexity depends on species identity and hunting strategy	63
Abstract.....	64
Introduction.....	65
Materials and methods.....	68
Results.....	73
Discussion	81
References	89

Chapter 4: General discussion.....	96
The diet of spiders in rice-paddy ecosystems during the cropping season	96
Gnats and midges during the cropping season	96
Planthoppers and leafhoppers during the cropping season	97
The diet of spiders during the cropping season	98
Effects of landscape complexity on the diet of spiders and their prey in rice-paddy ecosystems	101
Midges in rice-paddy ecosystems of different habitat complexity	101
Planthoppers and leafhoppers in rice-paddy ecosystems of different habitat complexity	102
Spiders in rice-paddy ecosystems of different habitat complexity	103
Recommendations to strengthen biological control by spiders.....	106
Conclusion.....	106
References	109
Appendix A	115
Appendix B	118
Appendix C.....	120
Appendix D	123
<i>Acknowledgements</i>	125
Curriculum vitae	127
List of publications	129

Abstract

Rice is the most important staple crop of the world, providing approximately 19% of the world population's caloric uptake and being cultivated on 163 million ha. Rice provides food and income to an estimated 200 million rice farmers and their families and is deeply ingrained in many social cultures worldwide. While the green revolution has led to an impressive increase in yields the input of agrochemicals has resulted in new problems, such as reoccurring outbreaks of rice insect pests. To evaluate the potential of biological control by generalist predators, such as spiders, in rice-ecosystems the diets of spiders were analysed over three consecutive sampling dates (chapter 2) and in three rice-ecosystems of different habitat complexity (chapter 3).

Spiders are important bio-control agents of rice insect pests such as planthoppers (Delphacidae) and leafhoppers (Cicadellidae). To investigate temporal changes in spider prey and variations in prey due to landscape structure around rice fields, carbon and nitrogen stable isotopes of rice field arthropods were analysed over three consecutive sampling dates during the rice cropping season. Initial isotope composition of gnats and midges emerging from submersed rice fields indicates a larval algae diet, while later values suggest a switch to rice-derived carbon. Initial $\delta^{13}\text{C}$ values of plant- and leafhoppers were higher in fields of rice-heterogeneous landscapes, indicating migration from source populations feeding on C4 grasses into rice fields; later their $\delta^{13}\text{C}$ values approached those of rice. Isotope values of web-building and cursorial spiders in the earliest samples indicate aquatic gnat and midge prey. The later shift toward terrestrial herbivore prey was more pronounced for small than for larger species and in rice paddies near permanent vegetation, indicating use of prey from the surrounding landscape. The results suggest that rice field spiders are supported by three

different carbon pools: (1) aquatic carbon originating from algae and (2) legacy carbon from previous growing cycles, both incorporated via between-season predation on gnats and midges, and (3) carbon from the current rice season incorporated via herbivore prey.

To investigate regional differences and variation in spider prey with landscape complexity and management intensity, we analysed carbon and nitrogen stable isotope ratios of rice field arthropods from three rice cropping regions in the Philippines. Research was conducted in the intensively managed, hilly lowland region Laguna, marked by additional fruit and vegetable cultivation, the intensively managed, lowland region Muñoz, characterized by high field sizes and less diverse cropping systems, and the low-intensity highland region Ifugao, known for its rice terraces. $\delta^{13}\text{C}$ values of adult midges indicated that they had consumed algae during development, but midge larvae also relied on rice-derived carbon, especially in Laguna. Plant- and leafhoppers across all regions relied primarily on rice-derived carbon, with planthoppers in Ifugao tending to additionally feed on alternative host plants. Isotope values of spiders indicated a mixed diet with carbon derived from both aquatic and terrestrial prey. In general, spiders in Laguna and Ifugao more heavily relied on aquatic-derived carbon from midges while those in Muñoz incorporated more terrestrial-derived carbon. Landscape diversity, number of habitat patches surrounding the field, connectivity of rice bunds and shape of rice fields significantly impacted the carbon sources and diet composition of spiders, but the extent varied among species. Cursorial wolf spiders (Lycosidae) consumed greater amounts of aquatic prey in Laguna and Ifugao with more complex landscapes, and fed more on terrestrial prey in the less complex landscape of Muñoz. The majority of web-building long-jawed spiders (Tetragnathidae) and orb-weaver spiders (Araneidae) relied on terrestrial prey in Muñoz and Ifugao, but primarily on aquatic prey in Laguna, pointing towards resource partitioning between feeding guilds.

In conclusion, increasing aquatic midge prey via mulching and provisioning of suitable habitats via vegetation management on bunds, integrating rice fields into heterogeneous landscapes and avoiding pesticides is likely to support high spider populations and thus strengthen biological control of pest species in rice paddies.

Zusammenfassung

Reis ist das wichtigste Grundnahrungsmittel der Welt, das etwa 19 % des Kalorienbedarfs der Weltbevölkerung deckt und auf 163 Millionen Hektar angebaut wird. Reis liefert Nahrung und Einkommen für schätzungsweise 200 Millionen Reisbauern und ihre Familien und ist in vielen sozialen Kulturen weltweit tief verwurzelt. Die grüne Revolution hat zwar zu beeindruckenden Ertragssteigerungen geführt, doch der Einsatz von Agrochemikalien hat neue Probleme mit sich gebracht, wie z. B. wiederkehrende Ausbrüche von Reisschädlingen. Um das Potenzial der biologischen Schädlingsbekämpfung durch generalistische Räuber wie Spinnen in Reisökosystemen zu bewerten, wurde der Speiseplan von Spinnen an drei aufeinanderfolgenden Probenahmeterminen (Kapitel 2) und in drei Reisökosystemen mit unterschiedlich komplexen Lebensräumen (Kapitel 3) analysiert.

Spinnen sind wichtige Akteure der natürlichen Bekämpfung von Reisschädlingen wie Spornzikaden (Delphacidae) und Zwergzikaden (Cicadellidae). Um die zeitlichen Veränderungen der Spinnenbeute und die durch die Landschaftsstruktur in der Umgebung von Reisfeldern bedingten Beuteschwankungen zu untersuchen, wurden die stabilen Kohlenstoff- und Stickstoffisotope von Reisfeld-Arthropoden an drei aufeinanderfolgenden Probenahmeterminen während der Reisanbausaison analysiert. Die anfängliche Isotopenzusammensetzung von Gnitzen (Ceratopogonidae) und Zuckmücken (Chironomidae), die aus submersen Reisfeldern auftauchen, deutet auf eine Ernährung mit aquatischen

Gnitzen und Zuckmücken hin, während spätere Werte auf eine Umstellung auf aus Reis gewonnenen Kohlenstoff hindeuten. Die anfänglichen $\delta^{13}\text{C}$ -Werte von Sporn- und Zwergzikaden waren in Feldern mit reisheterogenen Landschaften höher, was auf eine Migration von Ausgangspopulationen, die sich von C_4 -Gräsern ernähren, in Reisfelder hindeutet; später näherten sich ihre $\delta^{13}\text{C}$ -Werte denen von Reis an. Die Isotopenwerte von netzbauenden und freijagenden Spinnen in den frühesten Proben deuten auf aquatische Gnitzen und Zuckmücken als Beute hin. Die spätere Verlagerung auf terrestrische Herbivore war bei kleinen Arten ausgeprägter als bei größeren und in Reisfeldern in der Nähe von Dauervegetation, was auf die Nutzung von Beutetieren aus der umgebenden Landschaft hinweist. Die Ergebnisse deuten darauf hin, dass sich Reisfeldspinnen von drei verschiedenen Kohlenstoffquellen ernähren: (1) aus Algen stammenden aquatischen Kohlenstoff und (2) aus früheren Wachstumsperioden stammenden Kohlenstoff, die beide über die Prädation von Gnitzen und Zuckmücken zwischen den Anbauphasen aufgenommen werden, sowie (3) Kohlenstoff aus der laufenden Reissaison, der über Herbivore als Beute aufgenommen wird.

Um regionale Unterschiede und Variationen in der Beute von Spinnen in Abhängigkeit von der Komplexität der Landschaft und der Bewirtschaftungsintensität zu untersuchen, haben wir die stabilen Isotopenverhältnisse von Kohlenstoff und Stickstoff von Reisfeldarthropoden aus drei Reisanbaugebieten auf den Philippinen analysiert. Die Untersuchungen wurden in der intensiv bewirtschafteten, hügeligen Tieflandregion Laguna, die durch zusätzlichen Obst- und Gemüseanbau gekennzeichnet ist, in der intensiv bewirtschafteten Tieflandregion Muñoz, die sich durch große Feldgrößen und weniger vielfältige Anbausysteme auszeichnet, und in der gering intensiv bewirtschafteten Hochlandregion Ifugao, die für ihre Reisterrassen bekannt ist, durchgeführt. Die $\delta^{13}\text{C}$ -Werte adulter Zuckmücken wiesen darauf hin, dass sie sich während ihrer Entwicklung von Algen ernährt hatten, aber auch die Mückenlarven waren auf

Kohlenstoff aus Reis angewiesen, insbesondere in Laguna. Sporn- und Zwergzikaden waren in allen Regionen in erster Linie auf Kohlenstoff aus Reis angewiesen, wobei die Zwergzikaden in Ifugao dazu neigten, sich zusätzlich von anderen Wirtspflanzen zu ernähren. Die Isotopenwerte von Spinnen deuten auf eine gemischte Ernährung hin, bei der der Kohlenstoff sowohl von aquatischer als auch von terrestrischer Beute stammt. Im Allgemeinen ernährten sich die Spinnen in Laguna und Ifugao stärker von aquatisch gewonnenem Kohlenstoff aus Mücken, während die Spinnen in Muñoz mehr terrestrisch gewonnenen Kohlenstoff aus Herbivoren aufnahmen. Die Landschaftsvielfalt, die Anzahl der das Feld umgebenden Habitate, die Vernetzung von Reisfeldbegrenzungen und die Form der Reisfelder hatten einen erheblichen Einfluss auf die Kohlenstoffquellen und die Zusammensetzung der Nahrung der Spinnen, allerdings in unterschiedlichem Ausmaß je nach Art. In Laguna und Ifugao mit komplexeren Landschaften verzehrten freijagende Wolfsspinnen (Lycosidae) größere Mengen an aquatischer Beute, während sie sich in der weniger komplexen Landschaft von Muñoz mehr von terrestrischer Beute ernährten. Die Mehrzahl der netzbildenden Kieferspinnen (Tetragnathidae) und Radnetzspinnen (Araneidae) ernährte sich in Muñoz und Ifugao von terrestrischer Beute, in Laguna jedoch hauptsächlich von aquatischer Beute, was auf eine Aufteilung der Ressourcen zwischen den einzelnen Fressgilden hindeutet.

Zusammenfassend lässt sich sagen, dass die Erhöhung der aquatischen Beute durch Mulchen und die Bereitstellung geeigneter Lebensräume durch die Bewirtschaftung der Vegetation auf den Reisfeldern, die Integration der Reisfelder in heterogene Landschaften und den Verzicht auf Pestizide wahrscheinlich hohe Spinnenpopulationen begünstigen und damit die biologische Kontrolle von Schädlingsarten in Reisfeldern stärken.

Chapter 1: General introduction

Rice

A brief introduction to the importance of rice

The origins of rice (*Oryza sativa*, Poaceae) domestication and cultivation date to approximately 13,500 years. Evidence for the use of cultivated rice has been discovered in Non Nok Tha, Thailand, dating back to 10,000 B.C. The earliest traces of rice cultivation in China are believed to be 8000 years old and were discovered at the middle Yangtze and upper Huai rivers; from there, it spread across China over the following 2000 years (GRiSP 2013). Puddling soil, i.e. watering soil to turn it into mud, and transplanting seedlings of rice from a separate seedbed to give rice plants a head-start, are assumed to have originated in China and contributed to the domestication and successful spread of rice (GRiSP 2013; Molina et al. 2011). Rice cultivation probably arrived in the Philippines and Indonesia 2000 – 1500 B.C. and continued to spread throughout Asia before being introduced into Africa and Europe around 300 B.C., into the Americas in the 17th century, and finally Australia in the 20th century, thus conquering all continents except Antarctica (GRiSP 2013; Greenland 1997).

Since its domestication from *O. rufipugon* (Molina et al. 2011), semi-aquatic, annual cultivated rice has fed more people over a longer period of time than any other crop (Greenland 1997). Today, rice is so ingrained into many Asian cultures that the phrase “Have you had your rice today?” is a common greeting in China, Korea and the Philippines, equivalent to “How are you?” in western cultures. In 2019/2020 over 492 million tons of rice were consumed globally comprising 19% of the world population’s caloric uptake, making rice the single most important staple crop in the world (Statista 2021; Elert 2014). Rice is currently cultivated in 116 countries and covers an area of 162 million ha, with Asia producing 90% of the global

supply (FAO 2021). However, only 7% of produced rice ever leaves the country of origin, indicating a profound amount of subsistence farming and the importance of rice as source of food and income to an estimated 200 million rice farmers and their families worldwide (GRiSP 2013; Greenland 1997; Fairhurst and Dobermann 2002).

Rice biology and cultivation

Rice prefers tropical conditions for growth, reaching heights from 0.4 to 5 m in a 3–6 month growing season, depending on variety and cropping system (GRiSP 2013). Several tillers emerge from the base of each stem, which in turn bear several panicles and flowering spikelets that develop into the grain after self-pollination (GRiSP 2013). Rice growth can be categorized into three phases: (1) a vegetative phase including germination, seedling and tillering stage, (2) a reproductive phase including panicle development, booting and flowering stage, and (3) a ripening phase in which the grain displays several sub-stages from “milky” over “dough” to “ripe”.

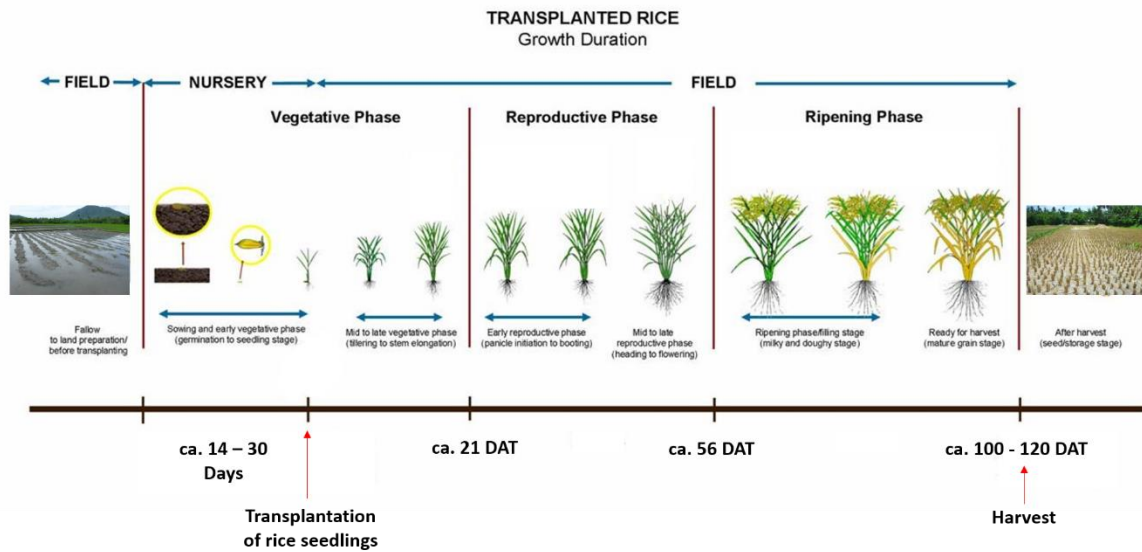


Fig. 1: Growth duration and phases of irrigated rice between field preparation and harvest (DAT = days after transplantation, adapted from IRRI 2022). Growth duration varies with rice variety.

Field preparation includes soaking, ploughing and puddling the soil, before levelling the field and application of manure or artificial fertilizer and possibly herbicides. After the flooding of the paddies, rice can be directly seeded or seedlings are transplanted from a seedbed into the field. Weeding and any application of agrochemicals (molluscicides, insecticides) usually takes place during the growth phase (GRiSP 2013; IRRI 2022). Rice cultivation can be categorized into four cropping systems, based primarily on the source and availability of water (Greenland 1997): (1) Rainfed lowland rice is prone to precipitation fluctuations, with water transport into and out of the paddy being most critical; (2) upland rice is rainfed, with paddies built on terraces of mountain slopes at risk of erosion and nutrient depletion; (3) irrigated rice, the most common cropping system, relies on channels and bunds to supply and conserve water

during dry seasons to avoid shortages; and (4) the flood-prone system utilizes sometimes uncontrollable flood water in river deltas to inundate rice plants.

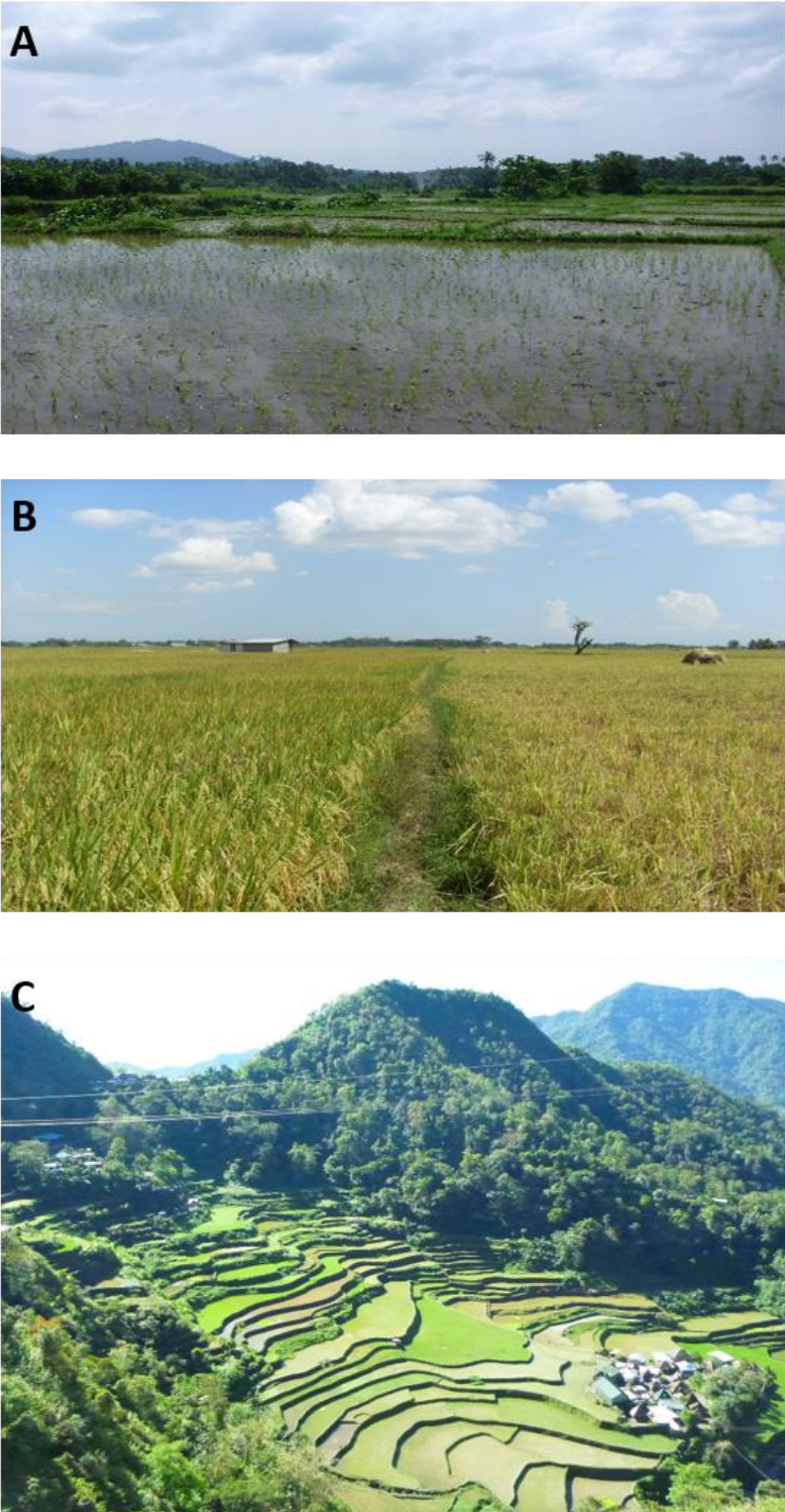


Fig 2: Rice fields within typical landscapes of (A) Laguna (PH1), (B) Nueva Ecija (PH2) and (C) Ifugao (PH3) during different growth stages.

Rice – a diverse agro-ecosystem

About 75% of rice cropping takes place on irrigated lowland fields, which can be subdivided into the paddy itself, the bund and the ditch or irrigation channel (GRiSP 2013; Bambaradeniya and Amarasinghe 2003). Such fields form a unique agronomically managed, temporary wetland ecosystem, harbouring a high diversity of microorganisms, fungi, plants (algae, herbs, ferns), vertebrates (mammals, birds, reptiles, amphibians and fish), and invertebrates such as spiders, insects, crustaceans, molluscs, annelids and nematodes (Roger et al. 1991; Fernando 1993; Bambaradeniya and Amarasinghe 2003). Although the waterbody of a rice field is drained occasionally, the surrounding channels form a more contiguous habitat from which aquatic organisms such as green algae, midge larvae (Chironomidae) and crustaceans can repeatedly recolonize the rice paddy and contribute to replenishment of organisms and nutrients (Roger et al. 1991; Kimura 2005). Bunds bordering the rice field comprise a more permanent component, sustaining terrestrial plants and organisms such as ants and hymenopteran parasitoids in this fluctuating environment (Way and Heong 2009; Fried et al. 2018; Dominik et al. 2018).

With the growth of rice plants, the rice paddy becomes more suitable for terrestrial herbivores such as planthoppers (Delphacidae), leafhoppers (Cicadellidae) as well as predators such as spiders (Ambalaparambil et al. 2005; Jayakumar and Sankari 2010; Betz and Tschardt 2017). The planthopper species *Nilaparvata lugens* and *Sogatella furcifera* are widely distributed in rice cropping regions of Southeast Asia and suck phloem sap at the base of the rice stem. Historically of no particular concern, they became particularly threatening to rice yields approximately ten years after the green revolution. At that time, mass occurrences induced “hopper burn”, an extensive loss on sap causing the plant to dry up. In addition, planthoppers

transmitted the grassy stunt disease virus resulting in yield losses up to ca. 7% or 150,000 tons in the Philippines in 1973 alone (Dyck et al. 1979).

Planthoppers, pesticides, problems

The green revolution after 1960 led to the intensification of agricultural practices, furthering high-input cultivation such as the use of mineral fertilizer and insecticides (Savary et al. 2012). While more potent agricultural input in combination with new rice varieties led to a remarkable 109% increase in rice yields of developing countries, new problems arose with the application of those practices (Pingali 2012). Shorter growth periods led to more crop cycles per year. Year-round monocultures degraded soils and resulted in loss of biodiversity.

Plant- and leafhoppers particularly benefit from nitrogen application to their host plant (Rashid et al. 2017). Artificially fertilized plants exhibit an increased amount of preferred amino acids which attract sap-sucking hemipterans and further stimulate planthopper feeding. This leads to increased fecundity and increasing populations. Heavy insecticide use, e.g. 4621 tons in the Philippines in 2019 (FAO 2021), enhances the development of insecticide resistance resulting in unstable populations and frequent outbreaks (Lu and Heong 2009; Khoa et al. 2019). Insecticides can even cause a shortened nymphal stage and a prolonged, fertile adult stage, thus creating a resurgence of the planthopper population and worsening the plant damage and potential yield loss (Chelliah and Heinrichs 1980). Critically, insecticides kill arthropods indiscriminately and particularly damage the ability of the rice field arthropod fauna to effectively exert biological control (Kiritani 1979; Cohen et al. 1994; Settle et al. 1996). With the threat of yield losses and the increasing knowledge of the devastating effects of insecticides, management practices should turn to methods that enhance biological control by one of the most abundant groups of arthropod predators: spiders.

Spiders

A brief introduction to spiders

With over 49,853 species belonging to 131 families, spiders (Araneae) are one of the most diverse and ubiquitous arthropod predators in the world. Spiders have conquered every possible niche on earth (Turnbull 1973). They occur in almost every terrestrial and some aquatic habitats except Antarctica and the open ocean (World Spider Catalog 2022; Foelix 2011). Spiders rank number seven of the most diverse animal groups after Acari, Hemiptera, Diptera, Lepidoptera, Hymenoptera and Coleoptera, and are considered one of the most diverse terrestrial predators of the world (Coddington and Levi 1991; Pekár and Toft 2015).

The first known true spider (Araneae) to produce spider silk was *Attercopus fimbriunguis*. This fossil was found in Upstate New York, USA, and dates to the Devonian age, 378 million years ago (Selden et al. 2008). The first record of spider silk is enclosed in a piece of amber, found in the United Kingdom and dating to the early Cretaceous period approximately 140 million years ago (Brasier et al. 2009). Spider silk has evolved to serve many purposes such as retreat-building, egg-protection, anchorage, movement, signalling and most importantly prey capture (Foelix 2011). Despite their huge evolutionary success, spiders, and their insect prey, suffered a dramatic decline in abundance over the last 40 years as was shown for the common orb-weaver *Araneus diadematus* (Araneidae), which only reaches a fraction of its former numbers in the Swiss midland (Nyffeler and Bonte 2020). This development must be reversed to maintain healthy natural and agro-ecosystems of which we, as humans, are part.

Spiders: ubiquitous generalist predators

Spiders are generalist predators with a wide range of potential prey groups, from arthropods such as insects and other spiders, to annelids and gastropods, as well as vertebrates like fish, frogs, lizards, birds and bats (Nyffeler et al., 2017; Nyffeler and Symondson 2001; Nyffeler and Knörnschild 2013; Nyffeler and Pusey 2014). Further, spiders vary their prey choice to ingest certain nutrients increasing fitness and fecundity (Uetz et al. 1999; Sigsgaard et al. 2001). Rare exceptions to the otherwise completely predatory lifestyle of spiders include the jumping spider *Bagheera kiplingi* (Salticidae), which uses Beltian bodies in acacia leaf tips as a supplemental food resource, and orb-weaving araneid (Araneidae) spiders that complement their diet with pollen sticking to their orb webs (Meehan et al. 2009; Eggs and Sanders 2013). A few spider families are specialists rather than generalists; pirate spiders (Mimetidae) and pelican spiders (Archaeidae) prey exclusively on other spiders by plucking threads of their target's web, mimicking prey or mating partners before attacking them (Foelix 2011; Wood and Scharff 2018). However, the vast majority of spiders are pronounced generalist predators with insects comprising the bulk of their food resources (Turnbull 1973).

Spiders use species-specific hunting strategies to capture their prey. Wandering spiders such as wolf spiders (Lycosidae), nursery-web spiders (Pisauridae) or lynx spiders (Oxyopidae) are active hunters, relying mainly on their sense of touch to detect vibrational cues that give away their prey's position (Uetz et al. 1999; Foelix 2011). Wolf spiders additionally use their good eyesight to orientate towards the prey. Once the prey is close enough, the spider dashes toward it, using its front legs to overwhelm it before biting with the chelicerae and injecting venom via their fangs. The prey is then often held in the air by the chelicerae so it cannot endanger the spider while struggling against the substrate. Feeding starts with chewing and exuding digestive juices when the prey is immobilised (Foelix 2011).

One of the most characteristic features of spiders is their ability to build webs. Web-building spiders pursue a sit-and-wait strategy to capture their prey (Olive 1982) with webs exhibiting various shapes and forms. Orb-weaver spiders (Araneidae) build vertically inclined actinomorphic webs whereas webs of long-jawed spiders (Tetragnathidae) are often inclined horizontally. Funnel-web spiders (Agelenidae) build sheet webs with a funnel-shaped burrow-like opening in which they hide. Dwarf spiders (Linyphiidae) wait upside down in horizontal sheet-webs attached to low vegetation or leaf litter combined with vertical signalling threads, but also resort to active hunting (Alderweireldt 1994; Uetz et al. 1999). The common goal of all web forms is to entangle potential prey and signal vibration its location to the spider for capture. Prey may be wrapped in silk for immobilisation and then bitten or vice versa. For example, *Nephila* bites first then wraps the prey whereas *Araneus* (both Araneidae) wraps the prey before biting it (Foelix 2011).

Spider silk also plays an important role in dispersal and colonization of habitats. Spiders disperse via “ballooning” by facing the wind, inclining their opisthosoma upwards from an exposed position and exuding a silk thread which lifts them upwards with the air current. Long-jawed spiders, orb-weaver spiders, crab spiders (Thomisidae) and dwarf spiders balloon as juveniles to escape overcrowding and cannibalism during spring time, whereas adult dwarf spiders start ballooning in high abundances during early autumn (Turnbull 1973; Foelix 2011). With this dispersal ability, spiders can travel distances over 1000 km (Bell et al. 2005). Dwarf and long-jawed spiders are also reported to sail by rising their front legs when they encounter both fresh and marine water, increasing their chances to survive, disperse, and colonize new habitats (Hayashi et al. 2015). Overall, as generalist predators combined with their good dispersal abilities, spiders make an important contribution to biological control in agro-ecosystems (Snyder et al. 2006).

Spiders in agro-ecosystems and their potential for biological control

Spiders are among the most diverse and abundant generalist predators in agro-ecosystems (Birkhofer, Entling and Lubin 2013). Spiders kill an estimated 400 to 800 million tons of prey annually, of which approximately 2% originate from annual cropland (Nyffeler and Birkhofer 2017). Spiders are considered important biocontrol agents, but the food web dynamics and the efficiency of pest suppression often depend on traits of both pest and spider species, as well as crop and climate conditions (Riechert 1999; Michalko et al. 2018, 2019). Cropping systems with high management intensity and practices, such as cutting and mechanical tillage, disturb habitats and can severely decrease abundance and diversity of generalist predators on arable land, impairing potential biological control (Ishijima et al. 2004; Thorbek and Bilde 2004). Pesticide use detrimentally affects biological control by disrupting top-down control of food webs and harming spider communities, in particular (Cohen et al. 1994; Maloney et al. 2003).

Nonetheless, spiders are able to rapidly recolonize disturbed habitats and sustain local populations despite rather poor prey availability, due to their good dispersal abilities and their generalist feeding mode (Öberg and Ekblom 2006). The impact of spiders on pest populations has been demonstrated for a number of spider and pest taxa under field conditions. Cursorial spiders have been shown to retard initial built-up of aphids (Aphididae) in winter wheat and, among other generalists, wolf spiders reduce populations of aphids and leafhoppers in maize fields (Lang et al. 1999; Birkhofer et al. 2008), while cursorial wolf and weaving dwarf spiders can reduce aphid populations by up to 58 % (Marc et al. 1999). In a spider removal experiment, insect pest populations significantly increased in the absence of spiders, but were efficiently suppressed by the full community of spiders with a variety of hunting modes (Riechert and Lawrence 1997). Diverse spider assemblages in apple orchards prey on multiple herbivore

groups at different life stages and can protect plants from crop damage (Marc and Canard 1997).

An increased diversity of generalist predators sometimes facilitates intraguild predation, decreasing effective herbivore suppression in arable systems (Wise 2006), but habitat complexity and alternative prey can mitigate or eliminate the negative effects on biological control (Riechert 1999; Langellotto and Denno 2006; Rickers et al. 2006). For this reason, it is crucial to account for the food web and the local arthropod community as a whole, when evaluating the effectiveness of generalist predators in agro-ecosystems (Polis and Hurd 1996; Polis and Strong 1996). This must also include arthropods living all or part of their life cycle in the litter layer or in soil, not just above-ground taxa.

Generalist predators in agricultural fields link above-ground herbivore and below-ground detritivore systems (Scheu 2001; Snyder and Wise 2001; Wise et al. 2006). This is underscored by the fact that additional mulching of arable fields increases detritivore populations, which provide alternative prey for generalist predators, resulting in increased predation rates on aphids (von Berg et al. 2010). Mulching also increases spider abundance and significantly reduces plant damage in garden systems (Riechert and Bishop 1990). In contrast, inhibiting the emergence of detritivores from forest soil leads to reduced spider abundances (Miyashita et al. 2003). Despite sometimes ambiguous findings regarding the efficiency of spiders in controlling insect pest densities in various cropping systems (Riechert 1999; Michalko et al. 2018), with adequate alternative prey, spiders in Asian rice-paddies can successfully suppress the built-up of pest populations and exert top-down control (Settle et al. 1996).

Spiders in rice-paddy ecosystems

Rice agro-ecosystems impose enormous temporal and spatial variation on the landscape scale, forming an ever changing mosaic of terrestrial and aquatic habitats, fallow and managed fields, and surrounding semi-natural habitats, causing dynamic fluctuations in arthropod populations (Schoenly and Cohen 1991; Schoenly et al. 1996; Bambaradeniya and Amarasinghe 2003). Tropical rice-paddies exhibit the highest arthropod diversity among agricultural systems, with predators and parasitoids comprising almost 50% of the arthropod fauna in Sri Lanka and over 64% in Indonesia (Wilby et al. 2006; Bambaradeniya et al. 2004; Settle et al. 1996). In fact, spiders are among the most abundant arthropod predators in tropical rice-paddy ecosystems and contribute to biological control of rice insect pests such as plant and leafhoppers (Heong et al. 1991, 1992; Sigsgaard 2007). Indeed, pest suppression by predators in rice fields was most effective compared to other environments (Michalko et al. 2019). Stable isotope analysis has linked this effect to increased detritivore abundances in the early cropping season providing alternative detritivore prey to sustain spider populations (Park and Lee 2006). Spiders temporarily rely on dipterans before turning on herbivores; the release of fruit flies (*Drosophila melanogaster*) into rice field-adjacent habitats significantly increased spider populations outside and, later, inside the field, leading to decreased herbivore populations (Kobayashi 1975; Ishijima et al. 2006).

Heterogeneous landscapes are paramount for a diverse assembly of predators and parasitoids, which may in turn effectively counter herbivore populations (Symondson et al. 2002; Tscharrntke et al. 2005; Westphal et al. 2015). Increased landscape complexity and more, smaller rice fields with an accordingly higher number of bunds lead to lower herbivore abundances in both lowland and upland rice cropping systems (Dominik et al. 2018). Environmentally friendly farming, including abstinence from insecticide use, benefits rice-field

spiders across feeding guilds, with a particularly strong increase in the abundance of wolf and long-jawed spiders in fields within 200 m of forested areas (Baba et al. 2018). Forests, ditches and fallow fields in the vicinity of rice fields all enhance spider populations by providing refuge, functioning as reservoir for predators ready to colonize rice-paddies (Baba and Tanaka 2016; Tsutsui et al. 2016; Baba et al. 2019). Conservation management of surrounding habitats, such as leaving bundles of slashed weed on bunds and maintaining nearby fallow fields, can foster spider abundance on crop-bearing rice-paddies and thereby enhance biological control (Maloney et al. 2003; Betz and Tscharrntke 2017).

Research objectives and thesis outline

Research for this thesis was conducted within the framework of the interdisciplinary project LEGATO (**L**and-use intensity and **E**cological **e**n**G**ineering – **A**ssessment **T**ools for risks and **O**pportunities in irrigated rice-based production systems; Settele et al. 2015). As described above, spiders are important biocontrol agents and antagonists of herbivore insect pests in a number of different agro-ecosystems including rice. However, it is difficult to disentangle the many factors that shape the rice food web and the role of spiders as generalist predators therein (Welch et al. 2012).

To assess the role of spiders in rice-paddy ecosystems, I used to stable isotope analysis (SIA). SIA has proven to be a useful tool in many different ecological studies on the trophic position of predators, herbivores and detritivores as well as the primary producers (reviewed in Vanderklift and Ponsard 2003; Tiunov 2007; Martínez Del Rio et al. 2009; Potapov et al. 2019). This method also enables identification of possible feeding-linkages to identify energy channel in which carbon is derived from one or several primary producers towards consumers such as herbivores or predators.

For the first chapter, I collected the most abundant generalist predators (spiders), herbivores (plant- and leafhoppers), detritivores (gnats and midges) and the primary producer of this ecosystem (rice) over three consecutive sampling dates during the rice cropping season in Laguna, Philippines and applied SIA to investigate temporal changes in the diet of spiders and their prey due landscape structure around rice fields testing the following hypotheses:

Spiders use emerging adult aquatic insects, such as gnats (Ceratopogonidae) and midges (Chironomidae), early in the rice-growing season

Spiders switch to herbivore pest species of rice later in the season

Rice-heterogeneous landscapes benefit spiders via increased prey availability from non-rice field habitats, thus raising the contribution of terrestrial prey to spider nutrition and thereby the efficiency of spiders as predators of rice pest species.

For the second chapter, I collect the same animal groups and rice in three regions of the Philippines, Laguna, Nueva Ecija and Ifugao, and apply SIA for a finer-scale investigation of the diet of spiders under varying habitat complexity and management intensity. This chapter addresses the following questions:

Are the basal food resources of spiders in different rice field ecosystems of aquatic or terrestrial origin?

Do basal food resources differ between highland and lowland rice cropping systems?

How does the landscape and vegetation surrounding a rice field influence the diet of spiders?

Together, these chapters quantify the contributions of terrestrial and aquatic prey to spider nutrition, linking increased prey availability from non-rice field habitats with the efficacy of spiders as predators of rice pest species. This is an important step in understanding the underlying rice-field food-web dynamics and the factors supporting biological control in general.

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Chapter 2: Spiders in rice-paddy ecosystems shift from aquatic to terrestrial prey and use carbon pools of different origin¹

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¹ 1 NR and SS conceived and designed the study. SV selected field sites and obtained permissions of farmers and municipal offices. NR conducted field sampling, species identification and sample preparation. TRH developed statistical models. NR and TRH analysed the data. NR, SS, TRH wrote the manuscript, SS and TRH provided editorial help. All authors contributed to revising the manuscript.

Abstract

Spiders are important bio-control agents of rice insect pests such as plant- and leafhoppers. To investigate temporal changes in spider prey and variations in prey due to landscape structure around rice fields, carbon and nitrogen stable isotopes of rice field arthropods were analysed over three consecutive sampling dates during the rice cropping season. Initial isotope composition of gnats and midges emerging from submersed rice fields indicates a larval algae diet, while later values suggest a switch to rice-derived carbon. Initial $\delta^{13}\text{C}$ values of plant- and leafhoppers were higher in fields of rice-heterogeneous landscapes, indicating migration from source populations feeding on C4 grasses into rice fields; later their $\delta^{13}\text{C}$ values approached those of rice. Isotope values of web-building and cursorial spiders in the earliest samples indicate aquatic gnat and midge prey. The later shift toward terrestrial herbivore prey was more pronounced for small than for larger species and in rice paddies near permanent vegetation, indicating use of prey from the surrounding landscape. The results suggest that rice field spiders are supported by three different carbon pools: (1) aquatic carbon originating from algae and (2) legacy carbon from previous growing cycles, both incorporated via between-season predation on gnats and midges, and (3) carbon from the current rice season incorporated via herbivore prey. In conclusion, fostering aquatic midge and gnat larvae, e.g. via mulching, and integrating rice fields into rice-heterogeneous landscapes likely strengthens biological control of pest species in rice paddies by supporting high populations of spiders between cropping seasons.

Key words: rice field, stable isotopes, generalist predators, biological control, rice insect pest

Introduction

Rice (*Oryza sativa*) is one of the most important staple crops in the world, providing food to almost half of the world population and making up 27% of the world populations' caloric uptake (FAO/UN, 2004). With an ever-growing human world population, food security therefore is of outmost importance for rice-growing countries of temperate and tropical regions, including the Philippines. The green revolution led to agricultural intensification promoting high-input cultivation practices, such as application of mineral fertilizers and pesticides (Savary et al. 2012). High nitrogen input promotes sap-sucking insect herbivores while insecticides may not only reduce pest species but also their natural enemies, such as spiders, thereby reducing biological control of planthoppers (Delphacidae) and leafhoppers (Cicadellidae) resulting in yield losses (Kiritani 1979; Settle et al. 1996; Rashid et al. 2017).

With more than 40,000 species, spiders (Araneae) are diverse and ubiquitous predators, with the majority of species following a generalist foraging mode and thereby having a broad spectrum of prey organisms (Foelix, 2011; Riechert and Lockley 1984). Their ability to hunt in a variety of habitats in combination with high abundance positions spiders as potentially effective biocontrol agents (Riechert 1999; Symondson et al. 2002; Wise 1993). Dispersal by running and ballooning allows spiders to colonize agricultural fields soon after disturbance due to agricultural practices such as ploughing and seed sowing. This applies in particular to tropical arable systems with multiple cropping cycles per year and asynchronous planting practice (Marc et al. 1999; Sunderland and Samu 2000). In fact, spiders are among the most abundant arthropod predators in tropical rice ecosystems and assumed to contribute to the control of pest species such as plant- and leafhoppers (Heong et al. 1991, 1992; Sigsgaard 2007).

With the ability to capture prey of different feeding guilds, including herbivores and detritivores, spiders may play an important role soon after planting rice fields when herbivore populations still are low. Generalist predators in agricultural systems such as spiders may link above-ground herbivore and below-ground detrital systems by using prey of both of these systems (Scheu 2001; Snyder and Wise 2001; Wise et al. 2006). Von Berg et al. (2010) showed increased predation rates on aphids in wheat fields by carabid and staphylinid beetles due to mulching (applying dead organic matter like crop residue to the field), and Miyashita et al. (2003) found reduced spider abundance when the emergence of detritivores from the soil was inhibited in forests. Settle et al. (1996) demonstrated that, besides avoidance of pesticides, availability of alternative prey from the detrital system is critical for enhancing and maintaining high abundances of generalist predators in rice fields.

The analysis of natural variations in stable isotope ratios allows insight into the trophic position and basal food resources of animals in aquatic as well as terrestrial systems (Minagawa and Wada 1984; Post 2002; Scheu 2002; Potapov et al. 2018). For example, stable isotope analysis (SIA) detected prey shifts of spiders following increased detritivore abundances after adding detritus to vegetable gardens (Wise et al. 2006). SIA of rice field arthropods suggests that spiders forage on aquatic midges (Chironomidae) early in the rice cropping season before shifting their diet to herbivore plant- and leafhoppers later in the season, but this has only been studied in a single temperate rice field without considering the wider spatial context (Park and Lee 2006). It is known that the structure and composition of surrounding habitats (hereafter, landscape structure) can alter food availability for spiders by providing additional prey from nearby ecosystems (Hambäck et al. 2016), potentially affecting their function as predators of rice field pest species.

In the present study we used SIA to investigate the structure of arthropod food webs and the role of spiders as generalist predators in paddy-rice ecosystems. Specifically, we investigated the following hypotheses: (1) Spiders use emerging adult aquatic insects, such as gnats (Ceratopogonidae) and midges early in the rice-growing season, before (2) switching towards herbivore pest species of rice later in the season, and (3) rice-heterogeneous landscapes benefit spiders via increased prey availability from non-rice field habitats, thus raising the contribution of terrestrial prey to spider nutrition and thereby the efficiency of spiders as predators of rice pest species.

Materials and methods

Location

The study was set up in Laguna Province, Luzon, Philippines on two pairs of fields investigated in the framework of the interdisciplinary LEGATO project (Settele et al. 2015). The study area in Central Luzon has a dry season from November to April and a wet season with a southwest monsoon from May to October (GRiSP 2013). Monthly mean temperatures in the study area (Los Baños, Laguna Province, Philippines) during the study period are 27.4 to 28.8°C (climate-data.org). The area is characterized by intensive irrigated lowland rice cropping alongside other farming systems, including fruit plantations and vegetable gardens. The studied rice fields were located between 121.36° to 121.41° E and 14.11° to 14.18° N at altitudes from 25 to 275 m above sea level. The size of the fields ranged from 820 to 2400 m² (Appendix A). Study fields were selected in two different landscape structures. More heterogeneous landscapes in which the focal rice field was embedded into a mixed landscape comprising vegetable gardens, extensively managed agroforests with fruit trees, or small unmanaged

forests, shrubs and grassland with the rice field area at a distance of 100 m around the focal rice field comprising a maximum of 30% rice, henceforth referred to as “rice-heterogeneous” landscape. Fields within more homogeneous landscape comprised a minimum of 50% rice fields at a distance of 100 m around the focal rice field and were dominated by intensively managed rice monocultures, henceforth referred to as “rice-homogeneous” landscape. Rice-homogeneous and rice-heterogeneous fields were located at least 300 m apart from each other and the distance between the two pairs was >15 km. The elevation gradient was independent of landscape structure assignments.

Sampling

Field sampling was conducted during the rainy season from June to August 2012. Samples were taken 13 to 14, 27 to 29 and 41 to 43 days after transplantation of rice seedling into the fields (termed as two, four and six weeks after transplantation, respectively). To capture a broad range of rice-field arthropods for SIA, three sampling methods were used at each sampling date: sweep net, dip net and suction sampler. Samples were taken at three locations within each field: margin, halfway between margin and centre, and centre. Sweep netting consisted of 30 beats through the rice canopy per field location with a 30 cm diameter net. Dip netting employed an 18 cm diameter net with 800 μm mesh size drawn along a 10 m transect per field location. Suction sampling with a modified leaf blower (Blower-Vac; Arida and Heong 1992) was used to catch arthropods from the lower part of the rice plant and the water surface. Samples were taken from an enclosure of 1 m height covering 0.25 m² surface area placed at the margin, halfway between margin and centre, and centre of the field, continuing as long as arthropods were detected in the enclosure. Captured animals were

transferred to plastic bags, killed by freezing at -20°C and then stored in 70% ethanol at -20°C until sorting and identification of gnats and midges, plant- and leafhoppers and spiders (Stehr 1987; Barrion and Litsinger 1994, 1995). Preservation in ethanol little affects $^{15}\text{N}/^{14}\text{N}$ values in arthropods, but can slightly enrich $^{13}\text{C}/^{12}\text{C}$ values although this effect is expected to be negligible because the treatment was consistent across all samples (Fabian 1998; Hogsden et al. 2017). Simultaneous to arthropod sampling, three rice plants were collected from the three different locations in the field. Rice plants were oven dried at 60°C for 48 h, frozen and stored at -20°C.

Stable isotope analysis

Larvae and adults of gnats and midges, plant- and leafhoppers, spiders and rice plants were dried at 60°C for 48 h. Large spiders such as tetragnathids (Tetragnathidae) were ground entirely and a subsample used for the analysis, while small species were used whole. Samples were transferred into tin capsules which were closed before analysis. SIA was carried out by a combination of an elemental analyser (NA 1110, CA-Instruments, Milano, Italy) coupled with an isotope mass spectrometer (Delta Plus, Finnigan MAT, Bremen, Germany; Reineking et al. 1993). Natural variations in stable isotope ratios were expressed using the δ notation as δX (‰) = $(R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}} \times 1000$, with X representing ^{13}C or ^{15}N , R_{sample} the $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ ratio of the sample and R_{standard} the respective ratios of the standard. Vienna Peedee Belemnite limestone and atmospheric nitrogen were used as standards for ^{13}C and ^{15}N , respectively. Acetanilide ($\text{C}_8\text{H}_9\text{NO}$, Merck, Darmstadt) was used for internal calibration.

Statistical analysis

Changes in the abundances of individual animal groups (gnats and midges, plant- and leafhoppers, spiders) with sampling date (2, 4, 6 weeks after transplantation) and surrounding landscape structure (non-rice dominated and rice-homogeneous) were analysed for sweep net samples only using generalized linear mixed models. Data for each taxon was examined separately to ensure they met assumptions. The models were specified with “abundance” as response variable and independent variables “date” and “structure” representing sampling date and surrounding landscape structure, respectively. The response variable was log-transformed and specified with Gaussian distribution for gnats and midges. Negative binomial and Poisson distribution were specified for plant- and leafhoppers. The variables “date” and “structure” were included as fixed factors whereas “location” (three sampling locations within the field plot) was included as random factor nested in “field”. Aikake Information Criterion (AIC) was used to compare models; models were simplified by progressively removing non-significant variables to obtain the minimal adequate model. Residual plots of the models were inspected visually for outliers. Differences between means were inspected using Tukey’s HSD test at $p < 0.05$.

Variations in carbon stable isotope ratios of gnats and midges, plant- and leafhoppers and spiders by sampling date were analysed using linear mixed-effects models. The dataset was non-orthogonal because not all species were equally represented at each sampling date. Prior to the analyses data were inspected for homoscedasticity (Fligner-Killeen test) and normality (Shapiro-Wilk test). The independent variables “date”, “taxon” (taxonomic order), “species” and “structure” were included as fixed factors, whereas “location” was included as random factor nested in “field”. AIC was used to compare models, which were simplified by

progressively removing non-significant variables to obtain the minimal adequate model. Residual plots of the models were inspected visually for outliers. Differences between means were inspected using Tukey's HSD test at $p < 0.05$.

Relative contributions of gnats and midges, plant- and leafhoppers to the diet of spider species were calculated for each sampling date and field using the Bayesian mixing model FRUITS version 2.1.1 Beta (Fernandes et al. 2014). Fractionation factors including standard deviation per trophic level were set to 0.47 ± 1.23 and $3.41 \pm 0.41\text{‰}$ for carbon and nitrogen, respectively after Vander Zanden and Rasmussen (2002). Values on the contribution of prey taxa to the diet of spider species were analysed using linear mixed-effects models after arcsine transformation. The dataset was non-orthogonal because not all spider species were equally represented at each sampling date. The independent variables "date", "spider species" and "structure" were included as fixed factors, whereas "field" was included as random factor. Data inspection prior to the analysis and model selection were conducted as described above. Statistical analyses were performed in R version 3.3.1 (R core team, 2016) and the packages *nlme* (Pinheiro et al. 2013), *afex* (Singmann et al. 2018) and *multcomp* (Hothorn et al. 2008). Figures were plotted using the R package *ggplot2* (Wickham, 2009).

Results

Abundance

The abundance of adult gnats and midges differed significantly between sampling dates, but the effect also varied with landscape structure with densities on rice-heterogeneous fields exceeding those on rice-homogeneous fields by 30.6% on average ($F = 43.1$, $p < 0.001$ for *date* x *structure*; $F = 29.5$, $p < 0.001$ for *date*; Fig. 1, Appendix A). We found high abundances of gnats

and midges two weeks after rice transplantation, averaging 1077 ± 653 (mean \pm SD) and 745 ± 396 individuals per sample in rice-heterogeneous and rice-homogeneous fields, respectively. By four weeks the abundance decreased to approximately half and by the final sampling date it declined to 15% and 25 % of week two abundance.

Further, plant- and leafhopper abundance also differed significantly between sampling dates and landscape structures ($F = 4.4$, $p < 0.001$ for *date x structure*; $F = 100.8$, $p < 0.001$ for *date*, Appendix A); on average it was 30.7% higher in rice-heterogeneous than in rice-homogeneous fields with the difference being more pronounced later in the season (Fig. 1). In contrast to gnats and midges, two weeks after rice transplantation the abundance of plant- and leafhoppers was low averaging 12 ± 4 and 14 ± 9 individuals per sample in rice-heterogeneous and rice-homogeneous fields, respectively. By week four they had increased strongly to an average of 243 ± 81 and 169 ± 55 individuals per sample, but in week six they declined by 20-25% in both rice-heterogeneous and rice-homogeneous fields.

Spider abundance also differed significantly between sampling dates ($F = 286.4$, $p = 0.001$ for *date*; Fig. 1, Appendix A), with the changes being similar in rice-heterogeneous and rice-homogeneous fields. Similar to plant- and leafhoppers, two weeks after rice transplantation spider abundance was low, averaging 30 ± 21 individuals per sample. Then, by week four the abundance increased more than threefold to an average of 109 ± 97 individuals per sample, but by week six dropped to about half.

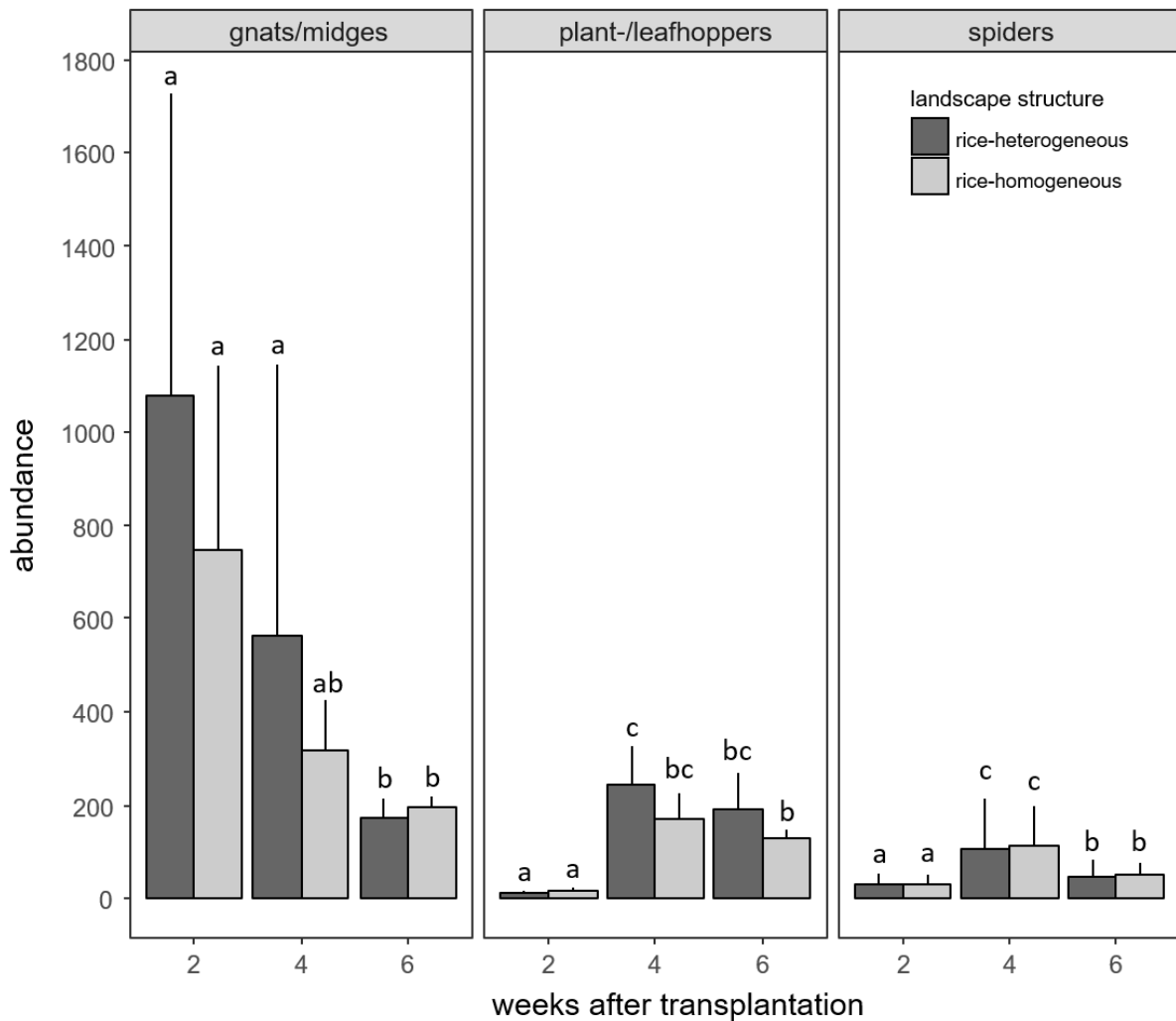


Fig. 1 Abundance (means \pm SD) of adult gnats and midges, plant- and leafhoppers, and spiders two, four and six weeks after transplantation of rice seedlings into the field in rice-heterogeneous and rice-homogeneous landscapes. Means not sharing the same letter differ significantly (Tukey's HSD test, $p < 0.05$).

Variations in $\delta^{15}\text{N}$ values

Two weeks after transplantation, rice had a $\delta^{15}\text{N}$ value of $4.3 \pm 0.7\text{‰}$ (mean \pm SD; Fig. 2, Appendix B). In larvae of gnats $\delta^{15}\text{N}$ values of $4.6 \pm 1.4\text{‰}$ were similar to those of rice. By contrast, $\delta^{15}\text{N}$ values of midge larvae averaged at $6.5 \pm 1.0\text{‰}$. With an average of $6.0 \pm 1.1\text{‰}$ $\delta^{15}\text{N}$ values of adult gnats exceeded those of the larvae, whereas values of adult midges

resembled those of the larvae and averaged $6.8 \pm 1.3\text{‰}$. $\delta^{15}\text{N}$ values were low in plant- and leafhoppers with values ranging between 0.6‰ (*Recilia dorsalis*, Cicadellidae) and $6.6 \pm 0.7\text{‰}$ (planthopper nymphs). As predators, spiders were most enriched in ^{15}N , with $\delta^{15}\text{N}$ values ranging between $7.7 \pm 0.6\text{‰}$ in *Araneus inustus* (Araneidae) and $8.6 \pm 1.0\text{‰}$ in *Atypena adelinae* (Linyphiidae).

After four weeks the $\delta^{15}\text{N}$ value of rice decreased by 2.3‰ (Fig. 2). The range of $\delta^{15}\text{N}$ values of plant- and leafhoppers narrowed and spanned from $2.2 \pm 1.3\text{‰}$ in leafhopper nymphs to $4.6 \pm 1.9\text{‰}$ in *Nephotettix nigropictus* (Cicadellidae). $\delta^{15}\text{N}$ values of gnats varied more than in week two, averaging $6.2 \pm 1.4\text{‰}$ and $3.5 \pm 1.4\text{‰}$ in adults and larvae, respectively. $\delta^{15}\text{N}$ values of adult midges and larvae were again similar, averaging $4.6 \pm 1.4\text{‰}$ and $4.6 \pm 1.2\text{‰}$, respectively. In spiders, $\delta^{15}\text{N}$ values remained high, but the range also narrowed to $6.3 \pm 0.7\text{‰}$ in *Dyschiriognatha hawigtenera* (Tetragnathidae) and $8.0 \pm 1.6\text{‰}$ in *Pardosa pseudoannulata* (Lycosidae).

Six weeks after transplantation, $\delta^{15}\text{N}$ values of rice increased to $5.5 \pm 0.4\text{‰}$ (Fig. 2). In plant- and leafhoppers, $\delta^{15}\text{N}$ values again varied little between $3.6 \pm 1.5\text{‰}$ in *R. dorsalis* and $4.9 \pm 1.1\text{‰}$ in *N. nigropictus*. $\delta^{15}\text{N}$ values of adult gnats decreased to $3.8 \pm 2.1\text{‰}$, but gnat larvae stayed almost constant at $3.7 \pm 2.1\text{‰}$. By contrast, $\delta^{15}\text{N}$ values of midge larvae and adults increased to an average of $5.4 \pm 1.6\text{‰}$ and $6.5 \pm 0.7\text{‰}$, respectively. The range of $\delta^{15}\text{N}$ values in spiders changed little being lowest in *Tetragnatha virescens* (Tetragnathidae) with $6.5 \pm 1.3\text{‰}$ and highest in *Tetragnatha maxillosa* (Tetragnathidae) with $7.5 \pm 0.9\text{‰}$.

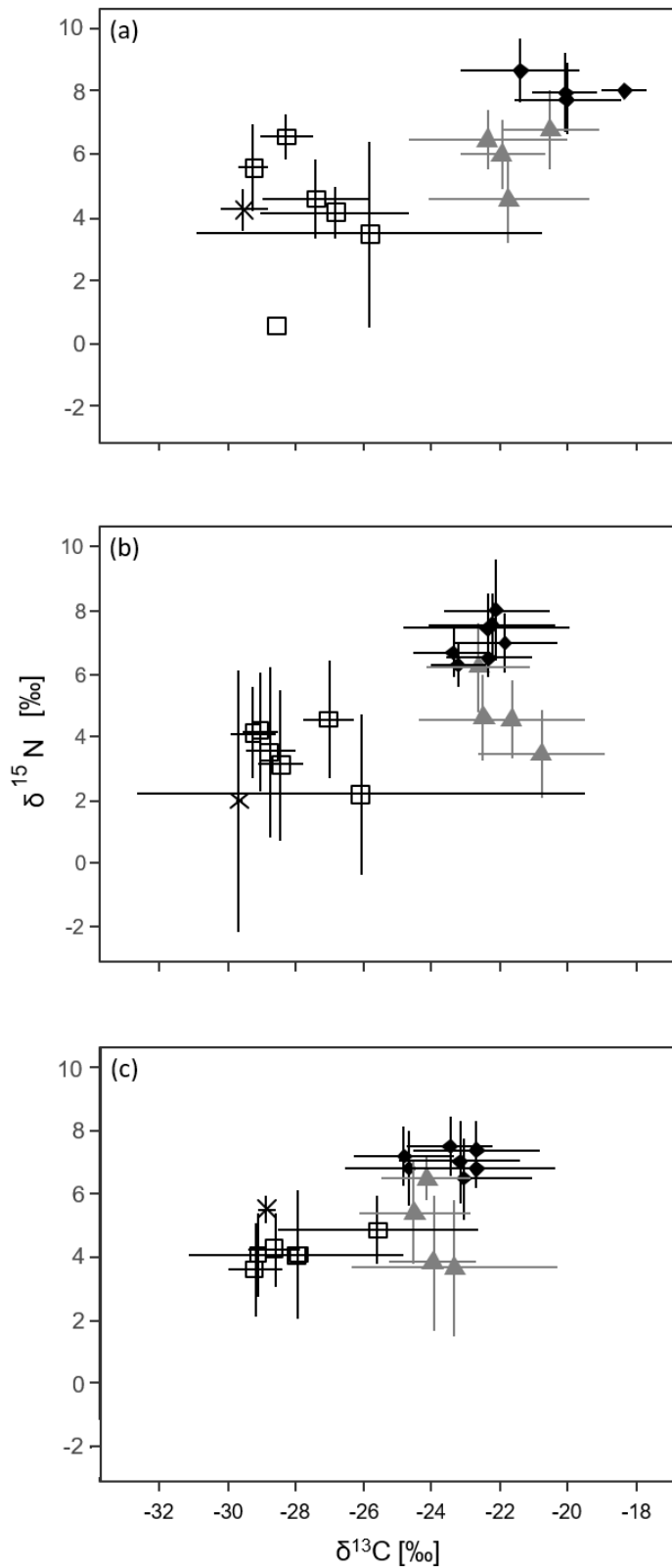


Fig. 2 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (means \pm SD) of rice (cross), spiders (filled circles), gnats and midges (triangles), plant- and leafhoppers (open squares) two (a), four (b) and six (c) weeks after transplantation of rice seedlings into the field.

Variations in $\delta^{13}\text{C}$ values

$\delta^{13}\text{C}$ values of both gnats and midges declined from two to four to six weeks after rice transplantation, with the decline in midges being significant between each sampling date, whereas in gnats only weeks two and six differed significantly ($F_{2,55} = 3.2$, $p = 0.0475$ for *date* x *species*; Fig. 3, Appendix A).

$\delta^{13}\text{C}$ values of plant- and leafhoppers differed significantly between sampling dates, but the effect depended on landscape structure ($F_{2,122} = 4.1$, $p = 0.0189$ for *date* x *structure*, Appendix A). $\delta^{13}\text{C}$ values generally declined later in the season, with the decline being more pronounced in rice-heterogeneous than rice-homogeneous fields (Fig. 3). Further, $\delta^{13}\text{C}$ values of plant- and leafhoppers varied significantly between species with the differences being independent of *date* and *structure* ($F_{5,122} = 24.0$, $p < 0.0001$ for *species*; Fig. 4, Appendix A). However, differences were mainly due to the cicadellid *N. nigropictus*; $\delta^{13}\text{C}$ values of this species significantly exceeded those of each of the other species.

As compared to plant- and leafhoppers, $\delta^{13}\text{C}$ values of spiders decreased more strongly with sampling date and the decline was more pronounced in rice-heterogeneous than in rice-homogeneous fields ($F_{2,109} = 5.0$, $p = 0.0086$ for *date* x *structure*; Fig. 3, Appendix A). Independent of sampling date and landscape structure, $\delta^{13}\text{C}$ values of spiders differed significantly between species ($F_{6,109} = 5.4$, $p = 0.0001$ for *species*; Fig. 4, Appendix A). They were low in the linyphiid *A. adelina* and the tetragnathid *D. hawigtenera*, and high in the araneid *A. inustus*, the lycosid *P. pseudoannulata* as well as the three tetragnathids *Tetragnatha javana*, *T. maxillosa* and *T. virescens*.

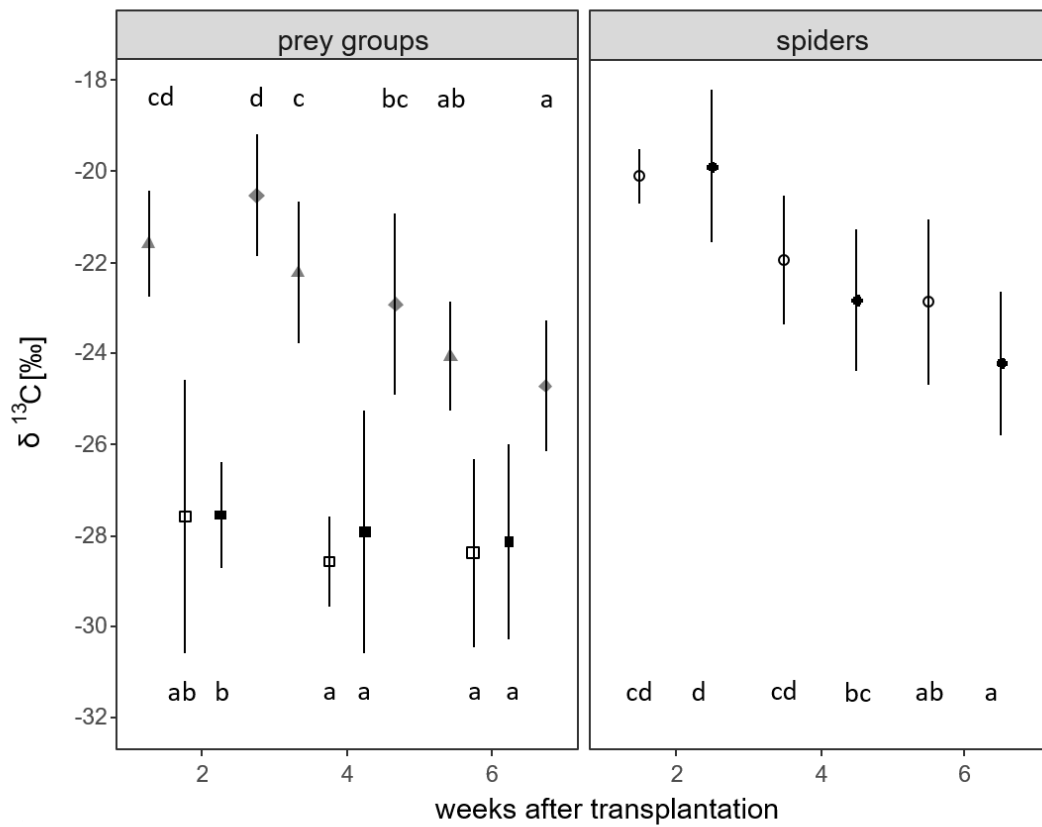


Fig. 3 $\delta^{13}\text{C}$ values of spiders (circles), gnats (triangles), midges (diamonds), plant- and leafhoppers (squares) in rice-heterogeneous (filled symbols) and rice-homogeneous (open symbols) fields two, four and six weeks after transplantation of rice seedlings into the field pooled for species (means \pm SD). Grey symbols represent groups pooled for rice-heterogeneous and rice-homogeneous fields. Means not sharing the same letter differ significantly (Tukey's HSD test, $p < 0.05$).

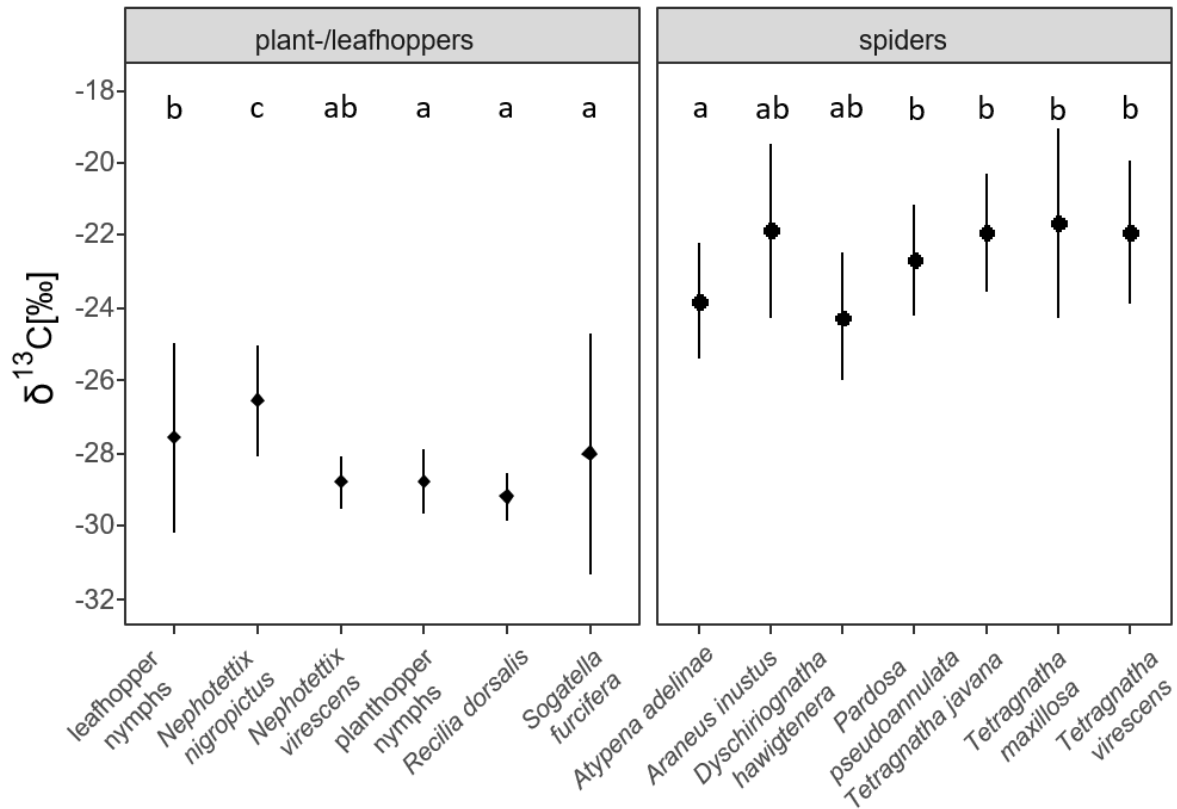


Fig. 4 $\delta^{13}\text{C}$ values of plant- and leafhopper species (Delphacidae: planthopper nymphs, *S. furcifera*; Cicadellidae: leafhopper nymphs, *N. nigropictus*, *N. virescens*, *R. dorsalis*) and nymphs and spider species (Linyphiidae: *A. adelinae*; Araneidae: *A. inustus*; Tetragnathidae: *D. hawigtenera*, *T. javana*, *T. maxillosa*, *T. virescens*; Lycosidae: *P. pseudoannulata*) pooled for sampling dates and rice-heterogeneous and rice-homogeneous fields (means \pm SD). Means not sharing the same letter differ significantly (Tukey's HSD test, $p < 0.05$).

Contributions of gnats and midges, and plant-and leafhoppers to the diet of spiders

The contribution of gnats and midges, and plant- and leafhoppers to the diet of spiders changed significantly with sampling date ($F_{2,42} = 310.9$, $p < 0.0001$ for *date*; Table 1, Appendix A). The percentage of gnats and midges decreased from an overall mean of $62.8 \pm 6.8\%$ to

61.7 ± 3.1% to 57.8 ± 5.5% at the first, second and third sampling, respectively. In parallel the percentage of plant- and leafhoppers increased from 37.2 ± 6.8 to 38.3 ± 3.1 to 42.2 ± 5.5%. The contribution of the two different prey groups to the diet of spiders did not vary with landscape structure, but in trend it varied among spider species ($F_{6,42} = 1.9$, $p = 0.0968$ for *spider species*; Table 1, Appendix A); resembling the pattern in $\delta^{13}\text{C}$ values, the contribution of plant- and leafhoppers to the diet of *D. hawigtenera* and *A. adelinae* (overall mean, pooled for sampling date 41.8 ± 7.4%) were higher than that in the other five species (overall mean, pooled for sampling date 38.1 ± 1.1%).

Table 1 : Contribution [% \pm sd] of gnats/midges and plant-/leafhoppers comprising the diet of spider species pooled landscape structure two, four and six weeks after transplantation (WAT) during the rainy season 2012 (for calculation see methods).

	2 WAT			4 WAT			6 WAT		
	gnats/midges	plant-/leafhoppers	\pm sd	gnats/midges	plant-/leafhoppers	\pm sd	gnats/midges	plant-/leafhoppers	\pm sd
Spider species									
<i>Atypena adelinae</i>	65.4	34.6	1.1	60.9	39.1	23.4	51.1	48.9	26.9
<i>Araneus inustus</i>	64.0	36.0	25.6	61.0	39.0	24.9	60.4	39.6	14.9
<i>Dyschiriognatha hawigtenera</i>	-	-	-	56.5	43.5	22.9	50.0	50.0	26.6
<i>Pardosa pseudoannulata</i>	-	-	-	65.2	34.8	23.9	65.6	34.4	23.9
<i>Tetragnatha javana</i>	66.6	33.4	27.0	62.3	37.7	22.7	57.8	42.2	26.9
<i>Tetragnatha maxillosa</i>	50.9	49.1	37.4	60.1	39.9	26.6	58.8	41.2	26.8
<i>Tetragnatha virescens</i>	67.2	32.8	25.9	65.6	34.4	22.2	60.6	39.5	26.3
mean	62.8	37.2		61.7	38.3		57.8	42.2	
sd	6.8	6.8		3.1	3.1		5.5	5.5	

Discussion

The arthropod communities of rice paddies are linked in a food web comprising of two main compartments - one being aquatic, based following the flooding of the rice fields, and the other being terrestrially, based with the transplantation of rice plants. Each compartment is formed by distinctive feeding linkages, but the terrestrial system is inextricably bound to the aquatic compartment by subsidies of emerging adult aquatic insects (Settle et al. 1996; Wilby et al. 2006). Changing prey availability during the cropping season results in marked changes in the terrestrial food web with plant- and leafhoppers becoming prey to terrestrial predators, in particular spiders, later in the season (Heong et al. 1991, 1992; Schoenly et al. 1996). These characteristics of the rice-paddy ecosystem were confirmed in this study by both population dynamics and SIA of the three most abundant arthropod groups, gnats and midges, plant- and leafhoppers, and spiders. The $\delta^{15}\text{N}$ values of these taxa spanned about 9 δ units, from 0.56 to 9.68‰. Assuming a trophic level fractionation of 2.5‰ between plants and herbivores and 3.4‰ between predators and animal prey (Vanderklift and Ponsard 2003), the rice-paddy food web comprised three to four trophic levels, aquatic polyphages, (gnat and midge larvae from the aquatic compartment), herbivores (leafhopper and planthopper nymphs and adults), and predators (spiders: tetragnathids, araneids, linyphiids and lycosids).

Aquatic polyphages

The abundance of gnats and midges markedly exceeded that of plant- and leafhoppers as well as spiders early in the rice-growing season. The fields studied were flooded during ploughing, levelling and fertilization prior to transplanting rice seedlings until about one week before harvest. Thus, midges and gnats could finish their larval phase and emerge as adults early during rice cropping, possibly even before rice transplantation (Clement et al. 1977). Higher

abundance in fields from rice-heterogeneous habitats in week two and four could be ascribed to the proximity of non-rice habitats which function as refuge from which fields can be recolonized more quickly after flooding compared to rice-homogeneous fields. Larvae of both gnats and midges are aquatic and live as decomposers on detritus and rice litter by grazing and filter feeding (Oliver 1971). Adult gnats live as ectoparasites on vertebrates and invertebrates (Papp and Darvas 1997), which potentially contributes to their enriched $\delta^{15}\text{N}$ values compared to larvae. Low variation in $\delta^{13}\text{C}$ values indicates nearly constant use of the same resources throughout the early cropping season. Adult midges do not feed and thus retain the larval stable isotope composition; in fact $\delta^{15}\text{N}$ values of midge adults and larvae were similar throughout the study period, decreasing only slightly in week four. High early season $\delta^{15}\text{N}$ values of midges indicate pre-season consumption of decaying plant material colonized by microorganisms, i.e. they are secondary rather than primary decomposers (Scheu and Falca 2000; Oelbermann and Scheu 2010). The pronounced changes in $\delta^{13}\text{C}$ values of midges also suggest a wide range of food resources, including detritus and algae ingested by grazing or filter feeding (Oliver 1971; Settle et al. 1996; Henriquez-Oliveira et al. 2003). Early in the season, rice plants are small and provide little shade to the field, promoting algal growth. $\delta^{13}\text{C}$ values of planktonic algae are typically less depleted than those of C3 plants, but may vary considerably. In well-aerated water bodies such as marine systems they are in the range of -20‰ (France 1995; Hambäck et al. 2016); algae from rice fields have $\delta^{13}\text{C}$ values of $-22.9 \pm 0.03\text{‰}$ (N. Radermacher, unpubl. data), which is consistent with gnats in our study and only slightly lower than midges. As rice plants increase in height, they increasingly shade the water body of the rice field and take up more nitrogen (Roger 1996; Fernández-Valiente and Quesada 2004), which presumably hampered algal growth at our study sites and may have induced a shift by gnats and midges from algae to detritus-based resources formed from rice

residues of previous cropping cycles (Johnson 1987; Galizzi et al. 2012). The decrease in $\delta^{13}\text{C}$ by approximately 2‰ in larvae and 4‰ in adults over the study period is in accordance with the findings of Park and Lee (2006) and points to a dietary shift from predominantly algae early in the season to more rice detritus-based resources later (detrital $\delta^{13}\text{C}$ values -28.2 ± 0.12 ‰; N. Radermacher, unpubl. data).

Herbivores

In tropical regions with asynchronous planting, like the study area, plant- and leafhoppers immigrate into rice fields from the surrounding vegetation throughout the cropping season, enabling planthopper females to start oviposition immediately after rice transplantation (Cook and Perfect 1985; Mollah et al. 2011). With an average egg development time of 8 to 11 days, plant- and leafhoppers are able to build up large populations within few weeks (Dyck et al. 1979). All three measures used in this study support early-season immigration and colonisation of rice fields from neighbouring plants. Abundance of plant- and leafhoppers significantly increased between two and four weeks after transplantation as immigrant-laid offspring matured. Results of the present study indicate that rice-heterogeneous landscapes, where rice fields are surrounded by gardens, grassland and forests, significantly increase colonization of rice fields by plant- and leafhoppers suggesting that these habitats function as refuges for rice insect pest species during fallow periods (Bambaradeniya and Edirisinghe 2008). While rice-heterogeneous landscapes presumably favour fast build-up of pest populations, plant- and leafhoppers also quickly colonized rice fields in rice-homogeneous landscapes, with their abundance four and six weeks after rice transplantation only 30.4% and 33.9% lower than in rice-heterogeneous landscapes, respectively. Overall, the results support earlier findings that the arthropod community on rice fields changes in abundance and

diversity during the cropping season (Heong et al. 1991; Schoenly et al. 1996; Wilby et al. 2006), with the decline in abundance of plant- and leafhoppers later in the season being likely due to predators, in particular spiders.

Planthoppers feed on basal plant parts while leafhoppers prefer aerial parts, such as leaves and leaf sheaths, but nymphs and adults of both taxa recovered in this study are known to preferentially suck phloem sap of rice (Dale 1994; Lu and Heong 2009). The considerable variation in week two $\delta^{15}\text{N}$ values reflects immigration from a variety of other vegetation, while the narrow range of $\delta^{15}\text{N}$ values later in the season indicates generations of plant- and leafhoppers that fed exclusively on rice. In contrast to herbivores feeding on bulk plant material, $\delta^{15}\text{N}$ values of phloem feeding insects typically match those of their host plants (McCutchan et al. 2003; Oelbermann and Scheu 2010), as phloem-feeding requires high nitrogen use efficiency resulting in low fractionation of ^{15}N in the consumer (Pinnegar et al. 2001; Vanderklift and Ponsard 2003).

$\delta^{13}\text{C}$ values presented the most nuanced picture, with significant variation over time, by distance between the rice field and other vegetation, and between species. Differences were greatest two weeks after rice transplantation, presumably due to colonisation of the rice fields from neighbouring habitats containing C4 grasses. C4 grasses are typically enriched in $\delta^{13}\text{C}$ caused by a different photosynthetic pathway resulting in distinct $\delta^{13}\text{C}$ values compared to C3 grasses (Fry 2006). While all of the plant- and leafhopper species found here feed preferentially but not exclusively on rice, the species effect was driven in large by *N. nigropictus*, which has the widest diet of any herbivore species collected. Its diet includes C4 plants such as *Echinochloa colona* and *Polytrias indica* (Dale 1994; Caton et al. 2010), found among the ruderal C4 grasses along field margins (Fried et al. 2018) and known to be used as additional food resources by *N. nigropictus* (Dale 1994; Schoenly et al. 2010).

Predators

Spiders were present in rice fields at low densities two weeks after rice transplantation and reached maximum abundance four weeks after transplantation. Above-ground growth of rice plants provides structural habitat complexity, known to be the major limiting factor for web building spiders (Cherrett 1964; Turnbull 1973; Rypstra 1983). Together with high prey availability, this presumably fostered the increased abundance of web building spiders including tetragnathids, araneids and linyphiids through week four. Six weeks after rice transplantation, the abundance of spiders significantly decreased. This may have been due to food shortage, suggested by decreased abundance of both prey types, combined with less effective prey capture by web-building spiders due to the denser rice canopy as well as predation and cannibalism (Olive 1982; Nentwig 1982; Wise 1993; Foelix 2011).

The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of most spiders closely matched those of gnats and midges, and less those plant- and leafhoppers, suggesting that they heavily relied on adult gnats and midges as food resources throughout the cropping season. This supports earlier findings that energy subsidies from aquatic systems may substantially contribute to the nutrition of terrestrial generalist predators (Sanzone et al. 2003; Gratton et al. 2008; Dreyer et al. 2012), and this also is confirmed by our mixing models. In particular early in the rice cropping season the contribution of gnats and midges to spider nutrition considerably exceeded that of plant- and leafhoppers, which is consistent with earlier suggestions (Settle et al. 1996; Park and Lee 2006). However, mixing models also confirmed that terrestrial prey, i.e. plant- and leafhoppers, substantially contributed to the diet of spiders. Overall, therefore the nutrition of generalist predators in rice fields resembles that of typical agricultural systems such as wheat fields where soil detritivores such as *Collembola* contribute to the diet of generalist

predators including spiders, thereby increasing biological control of herbivore pest species (Scheu 2001; Snyder and Wise 2001; von Berg et al. 2010). Notably, as indicated by lower $\delta^{13}\text{C}$ values later in the season the contribution of terrestrial prey to the diet of spiders in rice-heterogeneous fields exceeded that in rice-homogeneous fields, but this was not shown in the results of mixing models. This may reflect the generally higher density of plant- and leafhoppers in rice-heterogeneous compared to rice homogeneous fields. The higher contribution of terrestrial prey in rice-heterogeneous compared to rice homogeneous fields as indicated by $\delta^{13}\text{C}$ values suggests that rice-heterogeneous systems aggravate apparent competition between terrestrial herbivores and aquatic polyphages, where gnats and midges represent a donor controlled spatial subsidy to spiders contributing to strengthening biological pest control (Polis et al. 1997).

Stable isotopes revealed different diets at the species level with $\delta^{15}\text{N}$ values indicating two trophic levels of spiders, first- and second-order predators. Similar $\delta^{13}\text{C}$ values in the free-hunting lycosid *P. pseudoannulata*, the three web-building tetragnathids and the web-building araneid *A. inustus* suggest that the larger spider species predominantly fed on emerging gnats and midges. However, lower $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in *P. pseudoannulata* at week six indicate that terrestrial herbivore prey became increasingly important later in the season, as previously suggested (Ishijima et al. 2006; see above). Low $\delta^{13}\text{C}$ values in the linyphiid species *A. adelinae* and especially the tetragnathid species *D. hawigtenera* in weeks four and six, indicate that these species relied most heavily on terrestrial prey and these figures generally were confirmed by mixing models. High $\delta^{15}\text{N}$ values typical of second-order predators suggest that intraguild predation contributes significantly to spider nutrition (McNabb et al. 2001; Rickers et al. 2006), but this may be reduced by habitat complexity (Langellotto and Denno 2006; Sigsgaard 2007). In fact, maximum $\delta^{15}\text{N}$ values in week two suggest that intraguild predation

and cannibalism were more prevalent early in the cropping season, whereas growth of rice plants forming more complex habitats resulted in a decrease in $\delta^{15}\text{N}$ values in week four and six. Notably, in week two $\delta^{15}\text{N}$ values were highest in the linyphiid *A. adelina* suggesting that, despite its small body size, this species fed heavily on other predators including conspecifics, which is conform to earlier findings on linyphiid spiders (Vanacker et al. 2004; Park and Lee 2006). Although they do build webs, linyphiid spiders are also known to forage by hunting prey, thereby increasing their prey spectrum (Alderweireldt 1994; Uetz et al. 1999).

Conclusion

Changing prey availability during the cropping season resulted in spiders initially consuming insects emerging out of the aquatic system, then shifting gradually to terrestrial plant- and leafhopper prey later in the season, particularly in rice-heterogeneous fields. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of predators follow those of aquatic polyphages while simultaneously converging toward herbivore values. This suggests that terrestrial food resources became increasingly important for both aquatic polyphages and predators. In the present study nearby gardens, grassland and forests functioned as refuge from which plant- and leafhoppers colonized rice fields, thereby increasing the availability of terrestrial herbivore prey for spiders, as indicated by lower $\delta^{13}\text{C}$ values of spiders in fields with more heterogeneous landscapes later in the cropping season. Prey preference, however, appears to depend on spider species of which larger web-builders and free hunters feed more on aquatic prey compared to smaller web-building/wandering species feeding more on terrestrial prey.

Overall, our results suggest that generalist predators of tropical rice paddy fields are sustained by three different carbon sources. Early in the season they predominantly rely on carbon fixed by algae of the water body of rice fields (incorporated via gnats and midges), whereas later in

the season they predominantly rely on legacy carbon from previous growing cycles (incorporated via gnats and midges) as well as rice carbon of the current season (incorporated via herbivore prey). Alternative prey out of the aquatic system appears to be of paramount importance for fostering biological control of rice insect pest species. Further research, including experimental approaches investigating crop residue management practices, are necessary to elucidate potentials of enhanced biological control. Management strategies leaving more crop residue in the fields are likely to increase the availability of gnats and midges from submersed rice fields and therefore strengthen efficiency of biological control of rice insect pests. By contrast, the use of insecticides, particularly early in the season, reduces the availability of alternative prey and may critically compromise biological control of rice insect pest species by natural enemies in rice field ecosystems.

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Chapter 3: Variation in the diet of spiders in rice paddy ecosystems of different landscape complexity depends on species identity and hunting strategy

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Abstract

Spiders are important biological control agents for rice insect pest species, such as plant- and leafhoppers. To investigate regional differences and variation in spider prey with landscape complexity and management intensity, we analysed carbon and nitrogen stable isotope ratios of rice field arthropods from three rice cropping regions in the Philippines, the intensively managed, hilly lowland region Laguna, the intensively managed, lowland region Nueva Ecija with high field sizes, and the low-intensity highland cropping region Ifugao. $\delta^{13}\text{C}$ values of adult midges indicated that they had consumed algae during development, but midge larvae also relied on rice-derived carbon, especially in Laguna. Plant- and leafhoppers across all regions relied primarily on rice-derived carbon, with planthoppers in Ifugao tending to additionally feed on alternative host plants. Isotope values of spiders indicated a mixed diet with carbon derived from both aquatic and terrestrial prey. In general, spiders in Laguna and Ifugao more heavily relied on aquatic-derived carbon from midges while those in Nueva Ecija incorporated more terrestrial-derived carbon. Landscape diversity, number of habitat patches surrounding the field, connectivity of rice bunds and shape of rice fields significantly impacted the carbon sources and diet composition of spiders, but the extent varied among species. Cursorial lycosids consumed greater amounts of aquatic prey in Laguna and Ifugao with more complex landscapes, and fed more on terrestrial prey in the less complex landscape of Nueva Ecija. The majority of web-building tetragnathids and araneids relied on terrestrial prey in Nueva Ecija and Ifugao, but primarily on aquatic prey in Laguna, pointing towards resource partitioning between feeding guilds. In conclusion, increasing aquatic midge prey via mulching and provisioning of suitable habitats via vegetation management on bunds is likely to increase spider populations and thus biological control of pest species in rice paddies.

Key words: rice field, stable isotopes, generalist predators, biological control, landscape complexity

Introduction

With 492.7 million tons consumed globally in 2019/2020, rice (*Oryza sativa*, Poaceae) is the most important staple crop of the world, providing 19% of world caloric uptake (Statista, 2021; Elert 2014). Among other factors, rice yields can be threatened by severe outbreaks of insect pests, forcing farmers to resort to insecticides (Islam et al. 2012). In 2019, insecticide use in the Philippines alone amounted to 4621 tons (FAO 2021). With increasing insecticide tolerance in rice pests and the detrimental effects of insecticide application on rice field arthropod communities, especially detritivores and predators, research recommends cautious use of such tools and increasing focus on fostering natural enemy communities (Cohen et al. 1994; Park and Lee 2009; Khoa et al. 2019).

Spiders (Araneae), represented by over 40,000 species and consuming an estimated 400 – 800 million tons of prey per year globally, play an important role as predators in diverse biomes (Foelix 2011; Nyffeler and Birkhofer 2017). Spiders are abundant generalist predators exhibiting diverse hunting modes within a broad range of habitats, including arable fields, potentially posing an effective biocontrol against insect pest species (Wise 1993; Symondson et al. 2002; Michalko et al. 2019). Given their good dispersal abilities via running and ballooning, spiders are able to recolonize arable fields, disturbed by farming practices, from surrounding refuges as well as currently undisturbed fields, which is particularly effective in a landscape structure with asynchronous planting cycles, such as tropical rice fields (Marc et al. 1999; Sunderland and Samu 2000; Öberg 2007).

Spiders are among the most abundant predators in tropical rice fields and contribute to biological control by dwelling on herbivorous planthoppers (Delphacidae) and leafhoppers (Cicadellidae) (Heong et al. 1991, 1992; Sigsgaard 2000). As generalist predators, spiders link the above-ground/herbivore food web with the below-ground/detritivore food web by their ability to utilize prey originating from both systems (Scheu 2001; Snyder and Wise 2001; Wise et al. 2006). For example, the application of plant residues on a wheat field by mulching increased detritivores used as alternative prey by predators, thereby also increasing predation on herbivores (von Berg et al. 2012), whereas excluding detritivores emerging from forest floors reduced spider abundance (Miyashita et al. 2003). Indeed, alternative prey from the detrital system is crucial in maintaining high abundances of generalist predators in tropical rice fields (Settle et al. 1996). Although efficiency of herbivore predation by spiders can be decreased by intraguild predation scientific evidence shows, that abundant detritivores as an alternative prey can initiate pest suppression via fostering top down control (Polis et al. 1997; Henschel et al. 2001; Michalko et al. 2018).

A well-established method to explore the trophic position and basal food resources of animals in aquatic as well as terrestrial ecosystems is the analysis of natural variations in stable isotope ratios (Minagawa and Wada 1984; Post 2002; Kupfer et al. 2006). Stable isotope analysis (SIA) indicated that rice field-inhabiting spiders use different basal food resources by foraging on detritivorous, aquatic midges (Chironomidae) before shifting toward herbivorous, terrestrial plant- and leafhoppers on a single, temperate rice field (Park and Lee 2006), a trend confirmed on four tropical rice fields with different surrounding habitats (Radermacher et al. 2020). Landscape structure and composition of surrounding habitats can provide additional prey thus altering basal food resources to generalist predators and thereby affect the role of spiders as

rice insect pest antagonists (Polis et al. 1997; Hambäck et al. 2016; Dominik et al. 2018). The scale to which landscape structure may impact basal food resources of spiders is still unclear.

In this study, we investigated the influence of landscape features of different rice ecosystems on the diet of spiders and their role as biocontrol agents against rice insect pests. Therefore, we used SIA to investigate the following questions: (1) Are the basal food resources of spiders in different rice field ecosystems of aquatic or terrestrial origin? (2) Do basal food resources differ between highland and lowland cropping systems and (3) how does rice field-surrounding landscape and vegetation influence the diet of spiders?

Materials and methods

Study sites

The study was replicated in three regions in the Philippines: Laguna, Nueva Ecija and Ifugao Province, henceforth referred to as PH1, PH2 and PH3, respectively. All three regions are located on the island of Luzon, which has a dry season from November to April and a wet season with a southwest monsoon from May to October (GRISP 2013). Four fields per region were investigated in the framework of the interdisciplinary LEGATO project (Settele et al. 2015).

In PH1 (Los Baños, Laguna Province, Central Luzon, Philippines) monthly mean temperatures during the study period are 24.5 to 25.6°C (climate-data.org). The area is characterized by intensive irrigated lowland rice cropping, yielding two harvests per year, alongside other farming systems, including fruit plantations and vegetable gardens. The studied rice fields were located between 121.36° to 121.41° E and 14.11° to 14.18° N at an altitude of 25 m above sea level. The size of the fields ranged from 700 to 2760 m².

In PH2 (Muñoz, Nueva Ecija Province, Central Luzon, Philippines), monthly mean temperatures during the study period are 24.6 to 26.1°C (climate-data.org). The lowland farming system in the area is dominated by intensively managed, irrigated rice fields yielding two harvests per year. Vegetable cropping, fruit plantations and unmanaged forests, shrubs and grassland comprise a smaller share of land use compared to region PH1. The studied rice fields were located between 120.84° to 120.94° E and 15.61° to 15.67° N at an altitude of 25 m above sea level. The size of the fields ranged from 380 to 2240 m².

In PH3 (Banaue, Ifugao Province, northern Luzon, Philippines), monthly mean temperatures during the study period are 17.8 to 19.1°C (climate-data.org). This region is characterized by a

rain-fed low intensity highland rice cropping system which allows one harvest per year. Herb-covered stone walls and bunds follow the contours of the mountainous topography to form typically small, narrow rice terraces. Rice cropping areas are interspersed with forests and shrubs covering mountain tops, flanks and ridges. The studied rice fields were located between 121.06° to 121.13° E and 16.85° to 16.93° N at altitudes of 775 to 1075 m above sea level. The size of the fields ranged from 410 to 2400 m².

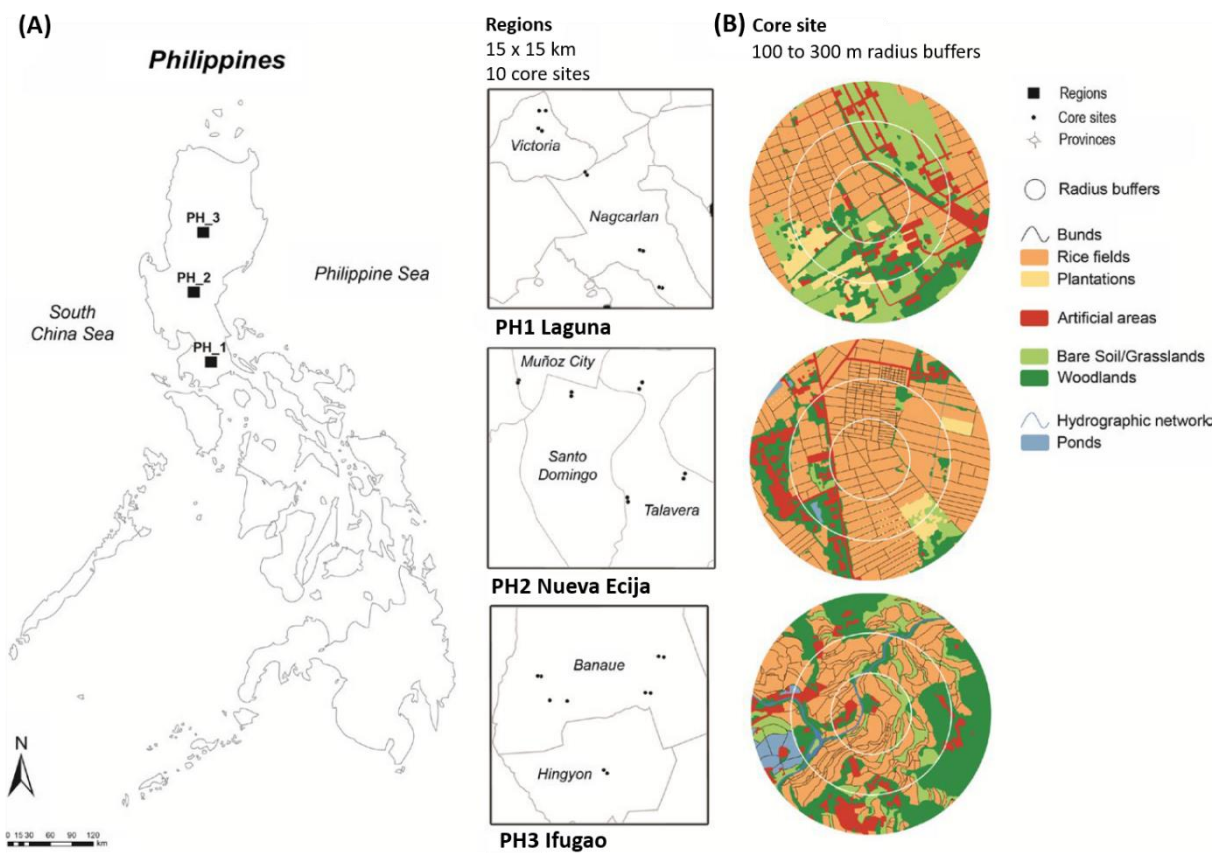


Fig. 1: Study area on Luzon, Philippines. **(A)** Locations of the 15 x 15 km regions in Laguna (PH1), Nueva Ecija (PH2), Ifugao (PH3). **(B)** Examples of mapped landcover properties within 100, 200, 300 m radii around core sites (adapted from Dominik et al. 2018).

Landscape metrics

The composition and configuration of the landscape was quantified by calculating four independent landscape metrics. Within a 300-m radius around each site, landscape features were identified and mapped using GIS-Software (ArcGIS 10.3, ESRI) and high-resolution SPOT-5 DIMAP images (2.5m), resulting in a classification of eight final categories: rice fields, woodlands, grasslands, artificial areas, plantations, rice bunds, hydrographic network, and ponds. The variable *SHDI* (Shannon Diversity Index) was used as a measure of compositional landscape heterogeneity, and quantifies the diversity of surrounding habitat patches. The number of rice patches (*NP*) was used as a measure of configurational landscape heterogeneity, and describes the rice habitat fragmentation within each landscape. In addition, two additional metrics of configurational landscape heterogeneity were calculated. The variable *COH* (patch cohesion index) represents the connectivity of terrestrial bunds between rice fields, and the variable *FRAC* (fractal dimension index) characterizes the shape complexity of the investigated field.

Sampling

Field sampling was conducted during the dry season from February to March 2013. Samples were taken 47 to 62, 45 to 47 and 46 to 54 days after transplantation of rice seedlings into the fields in PH1, PH2, and PH3, respectively. To capture a broad range of rice-field arthropods, three sampling methods were used at each sampling date, sweep net, dip net and suction sampler, and at three locations within each field, margin, halfway between margin and centre, and centre. Sweep netting consisted of 30 beats through the rice canopy per field location with a 30 cm diameter net. Dip netting employed an 18 cm diameter net with 800 µm mesh size drawn along a 10 m transect per field location. Suction sampling with a modified leaf

blower (Blower-Vac; Arida and Heong 1992) was used to catch arthropods from the lower part of the rice plant and the water surface. Samples were taken from an enclosure of 1 m height covering 0.25 m² surface area placed at each location within the field, continuing as long as arthropods were detected in the enclosure. Captured animals were transferred to plastic bags, killed by freezing at -20°C, then stored in 70% ethanol at -20°C until sorting and identification of midges, plant- and leafhoppers, and spiders (Stehr 1987; Barrion and Litsinger 1994, 1995). Preservation in ethanol little affects ¹⁵N/¹⁴N values in arthropods, but can slightly enrich ¹³C/¹²C values although this effect is expected to be negligible because the treatment was consistent across all samples (Fabian 1998; Hogsden and McHugh 2017). Simultaneous to arthropod sampling, three rice plants were collected from the three different locations in the field. Rice plants were oven dried at 60°C for 48 h, frozen and stored at -20°C.

Stable isotope analysis

Larvae and adults of midges, plant- and leafhoppers, spiders, and rice plants were dried at 60°C for 48h. Large spiders such as tetragnathids (Tetragnathidae) were ground and a subsample was used for the analysis, while individuals of small species were used whole. Samples were transferred into tin capsules which were closed before analysis. Stable isotope analysis (SIA) was carried out by a combination of an elemental analyser (NA 1110, CA-Instruments, Milano, Italy) coupled with an isotope mass spectrometer (Delta Plus, Finnigan MAT, Bremen, Germany; Reineking et al. 1993). Natural variations in stable isotope ratios were expressed using the δ notation as $\delta X (\text{‰}) = (R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}} \times 1000$, with X representing ¹³C or ¹⁵N, R_{sample} the ¹³C/¹²C or ¹⁵N/¹⁴N ratio of the sample and R_{standard} the respective ratios of the standard. Vienna Peedee Belemnite limestone and atmospheric

nitrogen were used as standards for ^{13}C and ^{15}N , respectively. Acetanilide ($\text{C}_8\text{H}_9\text{NO}$, Merck, Darmstadt) was used for internal calibration.

Statistical analyses

Average abundances per field were inspected by counting sweep net samples, pooled for location. Variations in carbon stable isotope ratios of midges, plant- and leafhoppers, and spiders were analysed using separate linear mixed-effects models for each group. Prior to the analyses, data for each group were inspected for homoscedasticity (Fligner–Killeen test) and normality (Shapiro–Wilk test). Each linear mixed-effects model was specified with $\delta^{13}\text{C}$ as response variable, *region*, *species* and their interaction as fixed factors, and *location* as random factor nested within *field*. Models were simplified by progressively removing non-significant variables to obtain the minimal adequate model with the lowest AICc. Residual plots of the models were inspected visually for outliers. To understand the effects of landscape characteristics, we analysed a series of new models with the same structure as above, plus one of the landscape metrics *SHDI*, *NP*, *COH* and *FRAC* at each of their three buffer distances (100, 200 and 300 m) as fixed factor. When a variable showed significant effects at more than one buffer distance, the most informative distance was selected by comparing AICc values. The dataset was non-orthogonal because not all spider species were equally represented in each study region; the spider family Linyphiidae was excluded from the linear mixed-effect models because it was not observed in all regions. We refrained from using rice as a covariate since $\delta^{13}\text{C}$ values were not significantly impacted by region ($F_{2,9} = 0.6$, $p = 0.5346$ for *region*).

Relative contributions of gnats and midges, and plant- and leafhoppers to the diet of individual spider species were calculated for each sampling date and field using the Bayesian mixing model FRUITS version 2.1.1 Beta (Fernandes et al. 2014). Fractionation factors including

standard deviation per trophic level were set to 0.47 ± 1.23 and $3.41 \pm 0.41\%$ for carbon and nitrogen, respectively, after Vander Zanden and Rasmussen (2001). Differences in the relative contributions of prey taxa to the diet of spiders were analysed using linear mixed-effects models (lme) as described above, with and without landscape metrics. Locations within each field were pooled and the random effect was simplified to field. Statistical analyses were performed in R version 3.6.1 (R core team, 2019) and the package *nlme* (Pinheiro et al. 2013). Figures were plotted using the R package *ggplot2* (Wickham, 2009).

Results

Abundance

Midges and spiders were by far most abundant in PH1 and least abundant in PH2, while plant- and leafhoppers were almost equally abundant in PH1 and PH3 but scarce in PH2. Midge abundance in PH1 averaged 92.91 ± 45.59 individuals per field (mean \pm SD, pooled for location), plant- and leafhoppers 49.00 ± 58.35 , and spiders 27.25 ± 15.03 individuals per field. In PH2, abundances were low in general, with midges and plant- and leafhoppers averaging 34.16 ± 24.21 and 9.25 ± 5.08 individuals per field, respectively. Abundances of spiders were lowest in PH2 averaging only 8.91 ± 6.12 individuals per field. In PH3 abundances of midges and plant- and leafhoppers were 251.83 ± 176.10 and 42.75 ± 53.90 individuals per field, respectively, and spider abundance was highest of any region, reaching 61.91 ± 21.21 individuals per field.

Variations in $\delta^{15}\text{N}$ values

In PH1, rice had a $\delta^{15}\text{N}$ value of $5.57 \pm 2.75\text{‰}$ (mean \pm SD; Fig. 2, Appendix D). Midge larvae (Chironomidae) showed $\delta^{15}\text{N}$ values of $7.02 \pm 1.59\text{‰}$, which were exceeded by adult midges averaging $7.54 \pm 0.97\text{‰}$. $\delta^{15}\text{N}$ values of planthoppers (*Sogatella furcifera*, Delphacidae) and leafhoppers (*Nephotettix virescens*, Cicadellidae) were similar to those of rice at 5.34 ± 1.33 and $5.25 \pm 1.38\text{‰}$, respectively. Spiders showed the highest enrichment in $\delta^{15}\text{N}$ with values ranging from $7.74 \pm 0.85\text{‰}$ in *Araneus inustus* (Araneidae) to $8.85 \pm 1.17\text{‰}$ in *Pardosa pseudoannulata* (Lycosidae).

In PH2, rice was least enriched compared to the other regions with $\delta^{15}\text{N}$ values averaging $3.61 \pm 0.88\text{‰}$. $\delta^{15}\text{N}$ values of midge larvae and adult midges were lower with $6.15 \pm 4.28\text{‰}$ and $5.31 \pm 1.43\text{‰}$, respectively. With $3.61 \pm 1.75\text{‰}$ planthoppers showed the lowest $\delta^{15}\text{N}$ values of all three regions, but matched those of rice in the region. Leafhoppers averaged at $2.87 \pm 1.33\text{‰}$. Region PH2 had the lowest $\delta^{15}\text{N}$ values for spiders, ranging between 4.43 ± 0.02 in *Tetragnatha nitens* (Tetragnathidae) to $6.87 \pm 0.94\text{‰}$ in *Atypena adelinae* (Linyphiidae).

In PH3, rice had $\delta^{15}\text{N}$ values similar to PH1 averaging $5.46 \pm 2.61\text{‰}$. Midge larvae and adults showed the lowest $\delta^{15}\text{N}$ values of all three regions with 3.61 ± 2.83 and $4.45 \pm 1.13\text{‰}$, respectively. Herbivore $\delta^{15}\text{N}$ values in this region were consistently lower than those of rice. Planthoppers in PH3 exceeded $\delta^{15}\text{N}$ values of those in PH2 slightly averaging $3.72 \pm 2.17\text{‰}$, whereas leafhoppers were the least enriched of all three regions with $2.20 \pm 1.02\text{‰}$. Spiders had relatively low $\delta^{15}\text{N}$ values similar to region PH2, ranging between $5.00 \pm 1.18\text{‰}$ in *Tetragnatha virescens* (Tetragnathidae) and $7.92 \pm 0.09\text{‰}$ in *Pardosa pseudoannulata*.

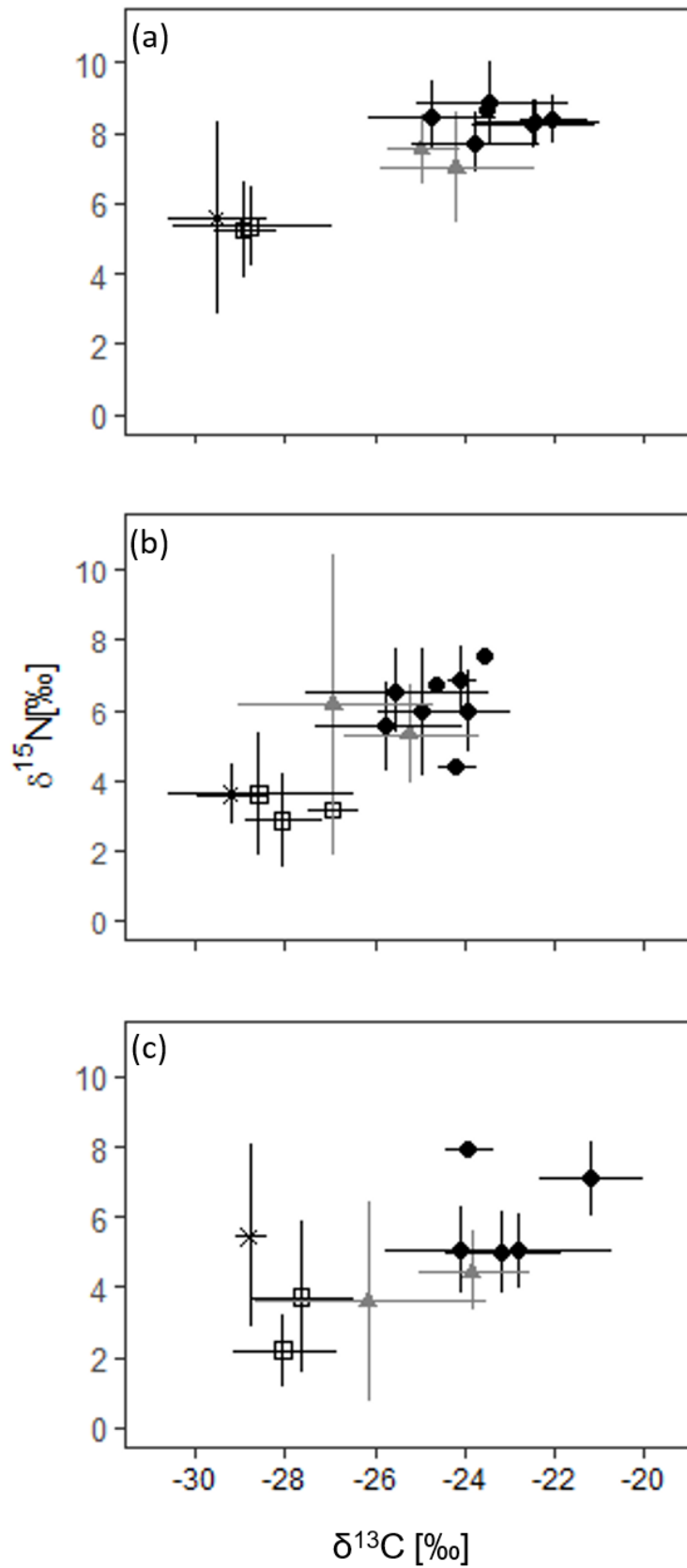


Fig. 2 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (means \pm SD) of rice (cross), spiders (filled circles), midges (grey triangles), plant- and leafhoppers (open squares) in regions PH1 (a), PH2 (b) and PH3 (c).

Variations in $\delta^{13}\text{C}$ values

$\delta^{13}\text{C}$ values of rice showed no significant differences between regions ($F_{2,9} = 0.6$, $p = 0.5346$ for *region*, Appendix C) averaging $-29.17 \pm 0.84\text{‰}$.

$\delta^{13}\text{C}$ values of midges differed significantly between regions, with midges in PH3 showing the highest values compared to PH2, where $\delta^{13}\text{C}$ values were the lowest of all three regions ($F_{2,9} = 4.4$, $p = 0.0476$ for *region*; Fig. 3, Appendix C).

$\delta^{13}\text{C}$ values of plant- and leafhoppers were significantly influenced by region ($F_{2,8} = 8.6$, $p = 0.0101$ for *region*; Fig. 3, Appendix C), increasing from PH1 to PH2 to PH3. $\delta^{13}\text{C}$ values of plant- and leafhopper species were significantly impacted by structural connectivity within a 300 m radius ($F_{1,37} = 1.8$, $p = 0.0050$ for *species* x *COH300*, Appendix C) and field shape within a 200 m radius ($F_{1,37} = 8.9$, $p = 0.0051$ for *species* x *FRAC200*, Appendix C).

$\delta^{13}\text{C}$ values of spiders in general as well as on species level were lowest in PH2 compared to PH1 with the highest values and varied significantly depending on region ($F_{8,69} = 3.5$, $p = 0.002$ for *region* x *species*; Figs. 3, 4, Appendix C). The most pronounced differences in $\delta^{13}\text{C}$ values between regions were shown by the tetragnathids *T. virescens* and *T. javana* followed by the araneid *A. inustus* compared to the rather constant $\delta^{13}\text{C}$ values of the lycosid *P. pseudoannulata*. Further, $\delta^{13}\text{C}$ values of spider species differed significantly depending on landscape diversity within a radius of 300 m ($F_{4,69} = 3.5$, $p = 0.0115$ for *species* x *SHDI300*, Appendix C). Structural complexity affected $\delta^{13}\text{C}$ values of spider species significantly within a 100 m radius ($F_{4,69} = 2.8$, $p = 0.0345$ for *species* x *FRAC100*, Appendix C).

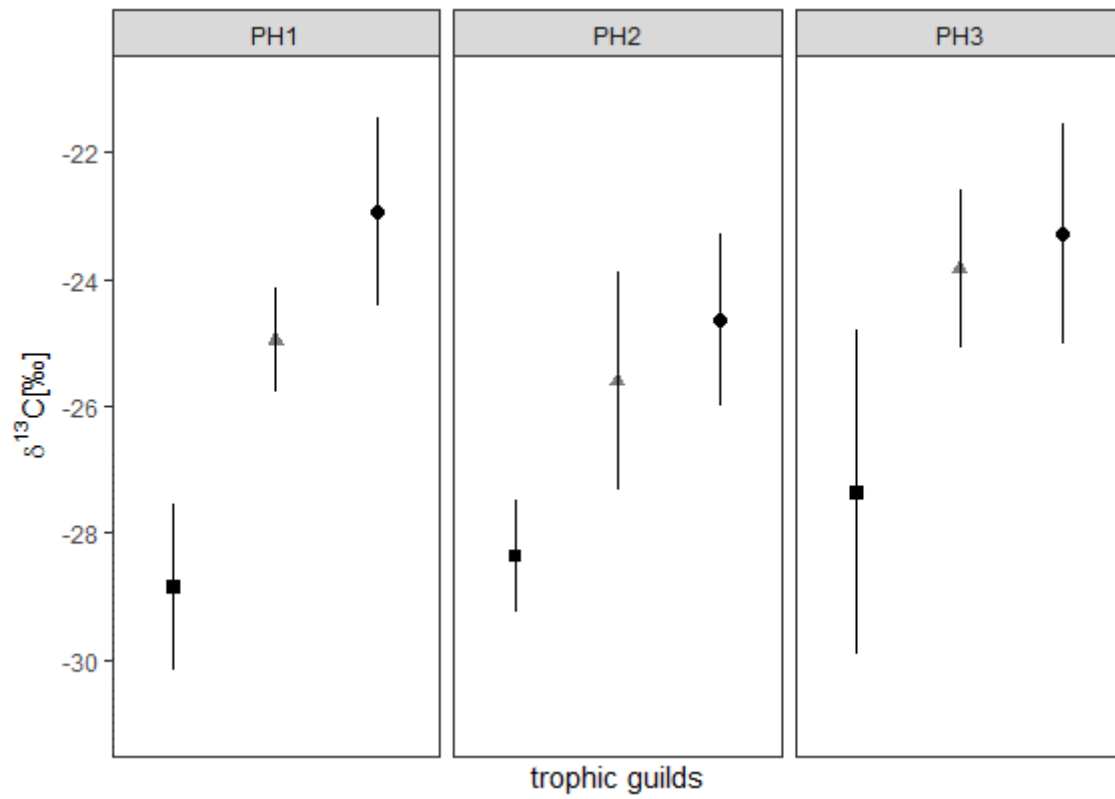


Fig. 3 $\delta^{13}\text{C}$ values (means \pm SD) of plant- and leafhoppers (black squares), midges (grey triangles) and spiders (black circles) in rice fields of the regions PH1, PH2 and PH3.

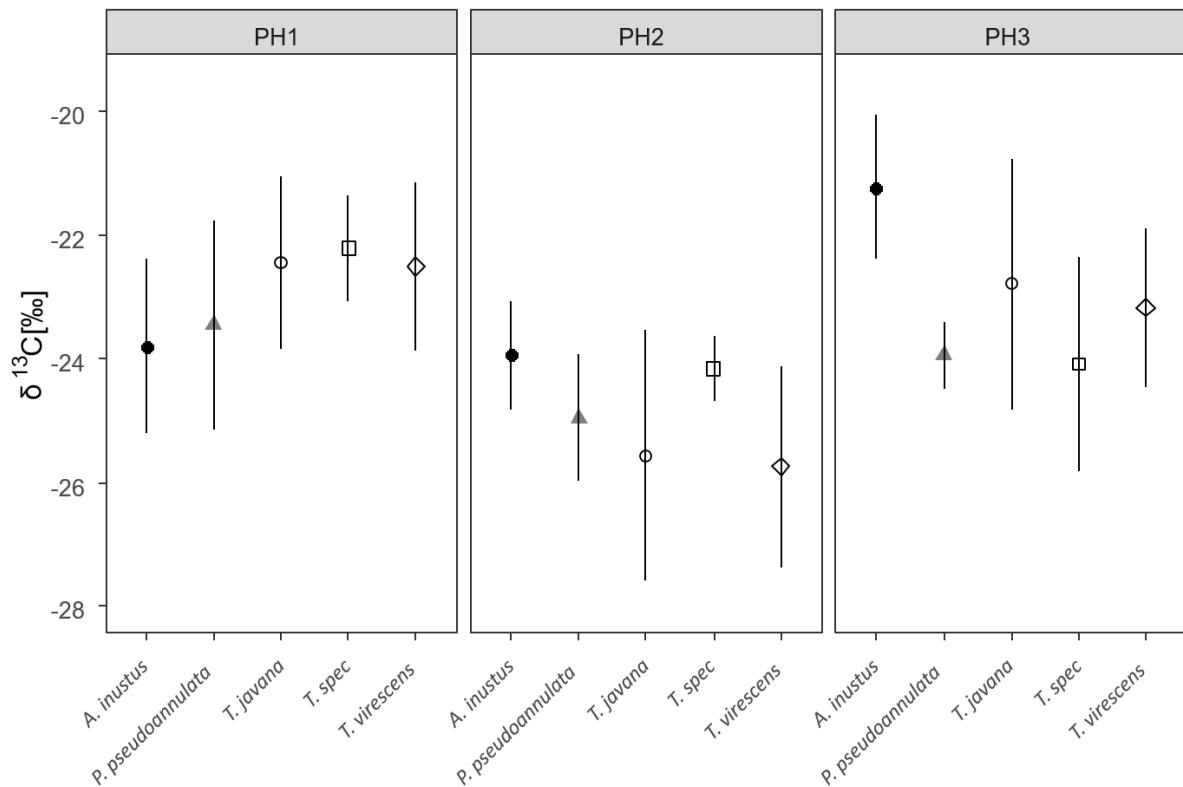


Fig. 4 $\delta^{13}\text{C}$ values (means \pm SD) of spider species *Araneus inustus* (Araneidae; black symbol), *Pardosa pseudoannulata* (Lycosidae; grey symbol), *Tetragnatha javana*, *Tetragnatha spec.* and *Tetragnatha virescens* (Tetragnathidae; open symbols) in rice fields in the regions PH1, PH2 and PH3.

Contributions of midges and plant- and leafhoppers to the diet of spiders

Contributions of midges and plant- and leafhoppers to the diets of spiders differed significantly with region depending on species ($F_{6,16} = 4.8$, $p = 0.0056$ for *region* \times *species*; Table 1, Appendix C). The percentage of midges decreased from an overall mean of 57.7 ± 22.0 to 53.2 ± 30.3 to $43.8 \pm 25.6\%$ in region PH1, PH2 and PH3, respectively. In parallel, the percentage of plant- and leafhoppers increased from 42.3 ± 22.0 to 46.8 ± 30.3 to $56.2 \pm 25.6\%$. The contribution of the two different prey groups also varied significantly with the number of patches within a 300 m radius around the focal field ($F_{1,8} = 6.7$, $p = 0.0319$ for *NP300*, Appendix

C) as well as with the connectivity between fields within a 100 m radius ($F_{1,8} = 6.0$, $p = 0.041$ for *COH100*, Appendix C). The contribution of plant- and leafhoppers to the diet of *A. inustus* and *T. virescens* (overall mean, pooled for sampling region $51.8 \pm 4.4\%$) was higher than in the other spider species (overall mean, pooled for sampling region $44.7 \pm 4.6\%$).

Table 1: Contribution [% \pm SD] of midges and plant-/leafhoppers to the diet of spider species in rice fields in the regions PH1, PH2 and PH3 during the dry season 2013 (for calculation see methods).

	PH1			PH2			PH3		
	midges	plant-/ leafhoppers	\pm SD	midges	plant-/ leafhoppers	\pm SD	midges	plant-/ leafhoppers	\pm SD
Spider species									
<i>Atypena adelinae</i>	47.7	52.3	23.2	77.7	22.3	12.1	-	-	-
<i>Araneus inustus</i>	45.2	54.8	21.7	34.5	65.5	18.5	96.9	3.1	0.8
<i>Pardosa pseudoannulata</i>	61.5	38.5	20.4	42.7	57.3	22.7	67.5	32.5	0.2
<i>Tetragnatha javana</i>	63.8	36.2	14.8	96.2	3.8	1.7	33.5	66.5	19.4
<i>Tetragnatha spec.</i>	75.1	24.9	15.5	41.3	58.7	15.4	31.8	68.2	16.8
<i>Tetragnatha virescens</i>	57.2	42.8	18.7	48.2	51.8	10.9	33.6	66.4	19.1
mean	57.7	42.3		53.2	46.8		43.8	56.2	
\pm SD	22.0	22.0		30.3	30.3		25.6	25.6	

Discussion

Aquatic polyphages

Adult and larval midges in PH1 showed the highest $\delta^{15}\text{N}$ values of all regions, with adults exceeding larval values by half a δ unit. Larval midges feed on detrital rice material and algae by filter feeding and grazing (Olivier 1971; Settle et al. 1996; Henriques-Oliveira et al. 2003), but adult midges do not feed, thereby retaining isotope values of their larval life stage with a slight enrichment of $\delta^{15}\text{N}$ originating from metamorphosis (Doi et al. 2007; Tibbets et al. 2008). High $\delta^{15}\text{N}$ values of both aquatic midge larvae and rice plants in PH1, suggest that midge larvae primarily fed on decaying plant material colonized by microorganisms, resulting in higher nitrogen enrichment typical of secondary decomposers (Scheu and Falca 2000; Oelbermann and Scheu 2010). Decaying rice plant material of the current and previous seasons is a ubiquitous food resource available to aquatic polyphages from the time of field flooding, before transplantation of rice seedlings and throughout the cropping season (Lawler and Dritz 2005; Schmidt et al. 2015). The mismatch between $\delta^{15}\text{N}$ values of rice and both adult and larval midges in PH3 suggests that the concurrently sampled rice plants do not reflect either current or previous food resources for these insects. This may be due to recent fertilizer application altering $\delta^{15}\text{N}$ values (Gealy and Gealy 2011) or the basal food resource of midges in PH3 originates from another source.

Regions differed significantly in $\delta^{13}\text{C}$ values of adult midges, but these differences were not correlated with any of the landscape metrics we tested. $\delta^{13}\text{C}$ values of adults in PH3 exceeded values of the larvae by ca. 2‰, pointing toward a shift of basal food resources between the adult and the larval generation of midges. This pattern was also observed to a lesser degree in PH2. In all regions, the higher $\delta^{13}\text{C}$ values of adult midges compared to rice plants indicates

reliance on algae during their larval stage earlier in the cropping season, which has been suggested earlier (Park and Lee 2006; Radermacher et al. 2020). $\delta^{13}\text{C}$ values of marine algae are in the range of -20‰ (France 1995; Hambäck et al. 2016), whereas rice field algae exhibit values of $-22.9\pm 0.03\text{‰}$ $\delta^{13}\text{C}$ (N. Radermacher, unpubl. data) consistent with $\delta^{13}\text{C}$ values of adult midges in our study. The independence of $\delta^{13}\text{C}$ values of midges from the landscape structures surrounding the rice fields may be explained by their feeding mode and life history. Adult midges can deposit eggs into water bodies such as inundated rice fields or, during fallow periods, into water-filled cavities (Olivier 1971). The larvae access food resources in their vicinity comprising algae and locally accumulated detritus, which are little affected by surrounding landscape features (Roger et al. 1991; Settle et al. 1996). This may be particularly relevant in PH3, the highland system with a single rice crop per year followed by extended fallow periods when algae likely form an abundant food resource in the shallow puddles and cavities where midges develop.

Herbivores

In regions PH1 and PH2, $\delta^{15}\text{N}$ values of plant- and leafhoppers closely resembled the values of rice at mid-season. Six to seven weeks after transplanting, tropical rice fields typically accommodate an established population of arthropods, including herbivores such as plant and leafhoppers, which preferably suck phloem sap of rice (Heong et al. 1992, Dale 1994). Fertilized rice plants provide high-quality, fitness-increasing food to plant- and leafhoppers, while their short reproductive cycles allow a new generation of plant- and leafhoppers to exclusively feed on rice plants (Dyck et al. 1979; Lu and Heong 2009). The need for efficient nitrogen use in phloem-feeding insects leads to $\delta^{15}\text{N}$ values characteristically resembling their host plant, due to low fractionation (McCutchan et al. 2003; Vanderklift and Ponsard 2003;

Oelbermann and Scheu 2010). However, this pattern was not observed in PH3, where *S. furcifera* and *N. virescens* were depleted by about 2.2 and 3.3 ‰, respectively, pointing to food resources other than rice. Mountainous climate conditions with lower mean temperatures, especially at night, slow insect egg and larval development (Chapman 1998). The resulting slower colonization of rice fields by plant- and leafhoppers from non-rice refuge vegetation results in herbivores reflecting isotope signatures of those alternative food resources at a later date compared to other regions (Schoenly et al. 2010; Radermacher et al. 2020).

The $\delta^{13}\text{C}$ values of plant- and leafhoppers varied significantly between regions, forming a gradient of increasing enrichment from PH1 to PH2 to PH3. Rice is clearly the most important food resource for rice-field plant- and leafhoppers in all three regions, but a moderate difference between $\delta^{13}\text{C}$ values of herbivores and rice plants and a high difference in $\delta^{15}\text{N}$ values point to the importance of non-rice host plants in region PH3. This is reflected in the significance of landscape factors in the $\delta^{13}\text{C}$ values of the plant- and leafhopper species. Both connectivity between rice fields and shape complexity of rice paddies within a radius of 200 m significantly influenced $\delta^{13}\text{C}$ values of plant- and leafhoppers on a species level. Although rice dominates the landscape in all three study regions, bunds, levees and small pathways between fields provide habitat for various herbs and grasses, with mountainous rice cropping regions having the highest plant species richness (Fried et al. 2018). These areas provide refuge and food resources to plant- and leafhoppers during fallow periods when rice is scarce (Bambaradeniya and Edirisinghe 2008; Gurr et al. 2011), altering $\delta^{13}\text{C}$ values (Radermacher et al. 2020). The effect is more pronounced in regions with more bunds, i.e. high connectivity, such as region PH3. Similarly, the increased perimeter-to-area ratio of complex-shaped rice fields results in longer bunds harbouring more non-crop plant species that herbivores can

potentially feed on. Differences in $\delta^{13}\text{C}$ values between herbivore species are to be expected as *Nephotettix* leafhoppers have a broader diet compared to planthoppers of the family Delphacidae (Dale, 1994; Caton et al. 2010), and potentially are even more strongly attracted to the complex plant volatiles emitted by non-crop plants masking rice odours (Randlkofer et al. 2010).

Predators

We detected regional differences in the diets of spiders, with $\delta^{13}\text{C}$ values indicating greater use of aquatic midges in lowland region PH1 and highland region PH3, and of terrestrial plant- and leafhoppers in the lowland region PH2. Prey derived from the aquatic system, often in the form of detritivore midges, constitutes the majority of spider food resources across various biotopes (Sanzone et al. 2003; Dreyer et al. 2012; Hambäck et al. 2016). However, spiders also rely on significant amounts of terrestrial herbivore prey (Heong et al. 1991, 1992; Radermacher et al. 2020).

Mixing models including both stable isotopes suggested prey preferences of spiders in different regions are highly species-dependent. The proportions of aquatic midges and plant- and leafhoppers for the nutrition of any particular spider species varied strongly between highland and lowland cropping regions. The variations were most pronounced in the tetragnathid *T. javana* and the araneid *A. inustus*, while the lycosid *P. pseudoannulata* showed less variation between regions. In PH1, web-building tetragnathids relied primarily on aquatic prey, but used more terrestrial prey in PH2 and PH3. The exception was *T. javana*, which in PH2 fed almost exclusively on aquatic prey. The araneid *A. inustus* showed the reversed pattern, using terrestrial resources in PH1 and PH2 while consuming almost only aquatic prey in PH3. In bigger fields, typical of PH2, maintaining complete inundation of paddies is more

difficult, leading to less aquatic habitat and an accordingly low availability of aquatic prey. *T. javana* builds webs above heights of one meter in tall grasses including rice, thus capturing midges more efficiently (Butt and Tahir 2010). General low prey availability in PH2 may have led to more intraguild predation, which is reflected in lower $\delta^{13}\text{C}$ values (Wise 2006).

Besides the factor region, landscape metrics had the greatest impact on spiders. Mountainous rice cropping areas, such as PH3, have higher plant species richness on rice field-surrounding bunds (Fried et al. 2018). Greater vegetation complexity combined with lower management intensity, as is typical for this region, results in higher diversity of prey and web-building spiders (Diehl et al. 2013). More food resources and habitat for plant- and leafhoppers in diverse bund vegetation in turn leads to web-building spiders feeding on more terrestrial prey. Web-building spiders have wider diet breadths compared to actively hunting spiders and partition resources by exploiting different strata, times and microhabitats (Butt and Tahir 2010). Araneids and tetragnathids build aerial orb webs pursuing a sit-and-wait strategy, whereas lycosids are actively hunting cursorial spiders (Uetz et al. 1999; Foelix, 2011). The passive hunting strategy of orb weaving araneids and tetragnathids means that relocation of the web is the only option to increase or alter their diet when prey is scarce or unsuitable (Olive 1982). Consequentially orb weavers have less influence over their prey, resulting in wider diets. By active hunting, however, lycosids, and to a lesser degree linyphiids, capture prey more selectively, leading to narrower ranges in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Thus hunting strategies, in addition to prey availability, impact spider nutrition and the utilization of aquatic and terrestrial resources (Wimp et al. 2013). Lycosids within the less complex landscape of region PH2 consumed more terrestrial herbivore prey, but mostly aquatic detritivore prey in the more complex landscapes of region PH1 and PH3, where fields are smaller. This suggests that *P. pseudoannulata* in PH2 primarily foraged in bunds, corroborating earlier findings of

lycosids preferring smaller fields, field margins and edges as habitat and hunting grounds (Öberg 2007; Öberg et al. 2007). *Pardosa* species are generally more abundant in less disturbed habitats with more vegetation complexity, but are also able to hunt on the water surface and thus thrive in a variety of habitats (Ishijima et al. 2004; Chen and Bernal 2011). That they consumed mainly terrestrial herbivores in PH2 may have been due to scarcity of alternative food resources, since plant- and leafhoppers are considered low-quality prey (Sigsgaard 2000).

The diversity and number of habitat patches within a radius of 300 m, field-shape complexity and connectivity of bunds significantly affected the diets of spiders in a species-specific way. This was underlined by both the $\delta^{13}\text{C}$ analysis and our mixing model showing a significant impact of these factors on the contribution of midges and plant- and leafhoppers to spider nutrition. Increasing numbers of patches increases predator activity and thereby biological control in agricultural landscapes (Bianchi et al. 2006). Seminatural and non-crop areas provide refuges against temporarily harsh within-field conditions during field preparation and early crop stages, creating spill-over effects in which predator and prey migrate into fields when plant growth improved habitat and food conditions for spiders and plant- and leafhoppers, respectively (Rand et al. 2006; Schmidt et al. 2008; Tsutsui et al. 2016). As generalist predators with good dispersal abilities, spiders benefit from increased habitat diversity at large spatial scales in a complex landscape due to increased species richness of potential prey (Symondson et al. 2002; Tscharntke et al. 2005; Marja and Tscharntke 2022). For example, tetragnathids and lycosids are more abundant in Japanese rice fields near ditches or forested areas, underscoring the positive effects of less disturbed habitats both as a refuge for spiders and a source of additional prey (Baba and Tanaka 2016; Baba et al. 2018, 2019).

Similarly, complex field shapes with an increased perimeter-to-area ratio result in smaller field sizes and provide more semi-natural habitat and resources to agrobiont arthropods, with differing implications for spider species according to functional traits such as body size, dispersal mode and hunting strategy (Rusch et al. 2015; Gallé et al. 2018, 2020). The spatial arrangement of crop fields and the degree to which they are interconnected with one another and with seminatural habitat also impacts populations of natural enemies, including spiders (Haan et al. 2020).

Conclusion

Stable isotope analysis indicated that both aquatic- and terrestrial-originating food resources provide important contributions to the diet of spiders in rice paddy ecosystems (question 1), but the effects are mediated by landscape factors and management practices rather than differing simply between lowland and highland regions (question 2). Spiders in the lowland cropping region PH1 rely on carbon of aquatic origin via algae-feeding midges, whereas terrestrial carbon from phloem-feeding plant- and leafhoppers is more prevalent in lowland cropping region PH2 and in highland cropping region PH3. However, high intraspecific variation in spider $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values between highland and lowland regions, as well as between the two lowland regions, underlines the fact that prey selection by spiders depends highly on species, hunting strategy and prey availability. The number and diversity of local habitat patches, connectivity of rice bunds and the shape of rice fields are paramount in shaping prey availability and spider nutrition (question 3). Spider diets are affected indirectly by different habitat types around rice fields, which provide diverse food resources and refuge to potential insect prey groups as well as to the spiders themselves. The abundance of plant-

and leafhoppers depends on the connectivity of bunds harbouring their host plants, ultimately influencing the diet of spiders in rice fields. Further effects on spider nutrition are mediated by habitat suitability and species-specific hunting strategies.

Overall, aquatic midges function as a staple food resource to spiders across all regions, while predation on terrestrial plant- and leafhoppers by spiders is greatest in low-intensity highland cropping regions and areas with increasing landscape complexity and denser vegetation. In these situations, spiders likely make an important contribution to biological control of rice insect pests. Further research investigating the management of crop residue to foster midges as early-season alternative prey and the ecological implications of bund vegetation management on herbivore populations will be necessary to fully understand the mechanisms underlying prey selection by spiders to ecologically engineer and enhance effective biological control.

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Chapter 4: General discussion

The diet of spiders in rice-paddy ecosystems during the cropping season

Gnats and midges during the cropping season

Gnats and midges are found consistently throughout the rice cropping cycle, with higher abundances in more heterogeneous landscapes. These dipteran families share an aquatic larval life stage which feeds by grazing, requiring only a freshwater supply and organic matter such as detritus or algae (Olivier 1971). Both requirements are fulfilled in rice-paddies at all phases of the cropping cycle. Residual rice material from previous cropping cycles, manure incorporated during field preparation, and flooding of the field stimulate oviposition by adult midges into the inundated field (Papp and Darvas 1997). Compared to rice-homogeneous habitats, higher abundances of gnats and midges in fields within heterogeneous landscapes indicate colonisation from refugia in semi-natural habitats. Decreasing abundance of gnats and midges during the rice growth phase is very likely due to increased predation in the aquatic and the terrestrial compartments of the rice-paddy food web (Heong et al. 1991a).

Food resources of gnat and midge larvae change during the cropping cycle. The flooded yet unplanted fields are an ideal habitat for green algae, providing gnat and midge larvae various food resources (Roger 1996; Fernández-Valiente and Quesada 2004). Because adult midges have reduced mouthparts and do not feed, their $\delta^{13}\text{C}$ values reflect the larval food resources, whereas adult gnats live as ectoparasites on vertebrates and invertebrates (Papp and Darvas 1997), resulting in higher $\delta^{15}\text{N}$ values in adults than larvae. C3 plants such as rice have $\delta^{13}\text{C}$

values around -29‰, marine algae in the range of -20‰ $\delta^{13}\text{C}$ (France 1995; Hambäck et al. 2016), but $\delta^{13}\text{C}$ values of algae in rice fields have -23‰ (N. Radermacher, unpubl. data). $\delta^{13}\text{C}$ values of adult gnats and midges collected at mid-season (Chapter 2) demonstrate that larvae preferentially feed on algae in the early phase of the rice cropping cycle. As rice plants grow and the canopy becomes denser, algal growth is hampered by shading and decreased nitrogen availability (Roger et al. 1991; Fernández-Valiente and Quesada 2004). Thus, gnat and midge larvae increasingly feed on detrital rice material as indicated by $\delta^{13}\text{C}$ values closer to those of C3 plants (Johnson 1987; Galizzi et al. 2012). High $\delta^{15}\text{N}$ values of adult and larval midges in the early season point to consumption of microorganisms colonizing decaying plant material, positioning them as secondary decomposers (Scheu and Falca 2000; Oelbermann and Scheu 2010). Lower $\delta^{15}\text{N}$ values later in the season reflect decreasing decomposition rates as the easily decomposable fraction of rice residues previous crop cycles is vanishing.

Planthoppers and leafhoppers during the cropping season

Plant- and leafhopper abundances in this study (Chapter 2) were conform to the general population dynamics observed in previous studies. Tropical conditions and asynchronous cropping sustain plant- and leafhoppers during fallow periods, enabling them to rapidly immigrate from older fields, as well as surrounding vegetation and semi-natural habitats into freshly planted rice fields (Bambaradeniya and Edirisinghe 2008). Early immigration and oviposition combined with short reproductive cycles, allow plant- and leafhoppers to build up large populations within weeks (Dyck et al. 1979; Cook and Perfect 1985; Mollah et al. 2011). Immigrant-laid offspring likely contributed to the fast population built-up in weeks four and six of this study, confirming earlier findings of temporal variation in hopper populations in rice fields, with the slight decline in week six attributable to predation (Heong et al. 1991a; Schoenly et al. 1996; Wilby et al. 2006).

Nymphs and adults of plant- and leafhoppers preferentially suck phloem sap of rice, with planthoppers preferring basal parts of the rice plant and leafhoppers preferring leaves and leaf sheaths (Dale 1994; Lu and Heong 2009). Phloem-feeding requires high nitrogen-use efficiency, resulting in low fractionation of ^{15}N and values close to those of the host plant (Pinnegar et al. 2001; Vanderklift and Ponsard 2003), whereas $\delta^{15}\text{N}$ values of herbivores feeding on bulk plant material typically exceed those of their host plants (McCutchan et al. 2003; Oelbermann and Scheu 2010). Thus, pronounced variability of $\delta^{15}\text{N}$ values in week two reflects immigration from various other host plants, while narrow $\delta^{15}\text{N}$ ranges later in the season indicates that the following generation of plant- and leafhoppers fed exclusively on rice. $\delta^{13}\text{C}$ values of plant- and leafhoppers varied significantly over time, by distance between rice and alternative vegetation and by species (Chapter 2). The greatest differences occurred two weeks after rice transplantation, when colonizing hoppers carried $\delta^{13}\text{C}$ values from natal semi-natural habitats containing C4 plants. Due to a different photosynthetic pathway C4 plants are more enriched in $\delta^{13}\text{C}$ than C3 plants depicting distinct, less negative values (Fry 2006). C4 grasses, such as *Echinochloa colona* and *Polytrias indica*, were found on bunds and in the field-surrounding areas of the study region (Fried et al. 2018). They belong to the feeding spectrum of the leafhopper *Nephotettix nigropictus*, which largely drove the effect indicating species-specific diets (Chapter 2), underlining that hoppers feed preferentially but not exclusively on rice (Dale 1994; Caton 2010; Schoenly et al. 2010).

The diet of spiders during the cropping season

Spider abundance was rather low two weeks after rice transplantation compared to their greatest abundance in week four, before declining in week six (Chapter 2). The majority of spider species found in this study are web-builders, such as long-jawed spiders, orb-weaver spiders and web-building/wandering dwarf spiders, for which structural habitat complexity,

as in mature rice plants, provides scaffolding for webs (Cherrett 1964; Turnbull 1973; Rypstra 1983). When rice plants are young and short and the space between rice plants wide, web-building is limited. Optimal structure is found after four weeks of rice growth; the dense canopy of later growth stages, together with reduced prey availability, intraguild predation and cannibalism, leads to a significant decrease in spider abundances (Nentwig 1982; Olive 1982; Wise 1993; Foelix 2011).

In general, the abundance of free-hunting spiders, like *Pardosa*, is higher in undisturbed habitats with more complex vegetation (Chen and Bernal 2011). The results of this study confirm that the wolf spider *Pardosa pseudoannulata* can effectively move between less disturbed margins and rice paddies, and is little affected by rice growth stage. This species is able to run and hunt on the water surface as well as on the lower foliage of plants, making it an early colonizer and important predator of insects throughout the season (Kiritani and Kakita 1975; Heong et al. 1991b; de Kraker et al. 1999; Bambaradeniya et al. 2004; Way and Heong 2009).

$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of spiders closely reflected those of gnats and midges, and to a lesser degree those of plant- and leafhoppers, indicating a strong reliance on aquatic gnat and midge prey throughout the cropping season (Chapter 2). This underscores the importance of aquatic subsidies to spider nutrition (Sanzone et al. 2003; Gratton et al. 2008; Dreyer et al. 2012; Hambäck et al. 2016). As in earlier studies (Settle et al. 1996; Park and Lee 2006), the contribution of aquatic detritivore prey is particularly high in the early season, exceeding that of terrestrial herbivore prey, which is not yet as abundant in the rice-paddy. Contributions of aquatic detritivore and terrestrial herbivore prey also resemble the nutrition of generalist predators of typical, solely terrestrial agricultural systems, such as wheat fields. In those situations, detritivore, soil-inhabiting Collembola provide alternative prey to generalist

predators and thus increase biological control of herbivore pest species (Scheu 2001; Snyder and Wise 2001; von Berg et al. 2010).

Mixing models also confirmed a substantial contribution of terrestrial herbivore prey to spider diets (Chapter 2). Lower $\delta^{13}\text{C}$ values later in the season suggest more predation on terrestrial herbivores in fields within heterogeneous landscapes compared to those in homogeneous landscapes, possibly reflecting the greater abundances of plant- and leafhoppers found in the more structurally diverse habitats. This finding, supported by $\delta^{13}\text{C}$ values, suggests that rice-heterogeneous habitats aggravate apparent competition in which gnats and midges represent a donor-controlled spatial subsidy to spiders, which in turn strengthens biological control (Polis et al. 1997; Henschel et al. 2001). In fact, decreasing detritivore prey availability, coincident with increasing herbivore prey availability, may induce a prey switch. This could represent a type-III functional response in which the predator population first is fostered by detritivore gnats and midges before preying on herbivore plant- and leafhoppers, thereby exerting top-down biological control (Marc et al. 1999; Maloney et al. 2003; Michalko et al. 2018).

Species-specific $\delta^{15}\text{N}$ signatures indicated two trophic levels of spiders, first- and second-order predators. Similar $\delta^{13}\text{C}$ values of the wolf spider *P. pseudoannulata*, the three long-jawed spiders *Tetragnatha maxillosa*, *Tetragnatha javana*, *Tetragnatha virescens* and the orb-weaver spider *Araneus inustus* suggest emerging gnats and midges as their predominant prey. Yet, the lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of *P. pseudoannulata* in week six indicate increasing importance of terrestrial prey later in the season, similar to previous observations (Ishijima et al. 2006). The compact habitus of the long-jawed spider *Dyschiriognatha hawigtenera* is unusual for this family, and in this study *D. hawigtenera* relied on terrestrial prey for half of its diet. In this way, it resembles the genus *Pachygnatha* of temperate zones, known to be

specialized on sap-sucking aphids (Harwood et al. 2005). The dwarf spider *Atypena adelinae* (formerly *Atypena formosana*) also relied heavily on terrestrial prey. It builds sheet-webs in the lower strata of the rice canopy, which it occasionally leaves for free hunting like other Erigoninae, making it well adapted for feeding on planthoppers hiding in that stratum (Alderweireldt 1994; Sigsgaard 2000; Harwood et al. 2003).

Maximum $\delta^{15}\text{N}$ values in week two suggest that intraguild predation and cannibalism contributed significantly to spider nutrition leading up to the rice cropping cycle. This was most notable in *A. adelinae*, and is not unusual for dwarf spiders (Vanacker et al. 2004; Park and Lee 2006). Intraguild predation can be reduced by habitat complexity and prey diversity (McNabb et al. 2001; Rickers et al. 2006), which is confirmed by decreasing $\delta^{15}\text{N}$ values in week four and six when rice plants were more developed.

Effects of landscape complexity on the diet of spiders and their prey in rice-paddy ecosystems

Midges in rice-paddy ecosystems of different habitat complexity

$\delta^{13}\text{C}$ values of midges differed significantly between regions but were not correlated to any of the tested landscape metrics (Chapter 3). Adult midges in Ifugao, and to a lesser extent in Nueva Ecija, showed enriched $\delta^{13}\text{C}$ values compared to larvae collected at the same time. This demonstrates a shift of food resources from algal diet in the older generation to a detritus-based diet in the younger generation, as previously found (Park and Lee 2006; Chapter 2). Sampling in Nueva Ecija and Ifugao occurred approximately seven weeks after transplantation

of rice seedlings, but eight weeks post-transplantation in Laguna. The similar $\delta^{13}\text{C}$ values of larvae and adults in Laguna indicate that algal growth had declined some time earlier.

It is unsurprising that midge diets were independent of landscape metrics. Midge larvae live in the vicinity of their detrital and algal food resources and are little affected by surrounding landscape structure (Roger et al. 1991; Settle et al. 1996). In the highland system Ifugao, the climate is colder, rice grows slower, and the cultivation cycle includes extended fallow periods, which likely give algae more time to develop in shallow puddles and cavities.

Planthoppers and leafhoppers in rice-paddy ecosystems of different habitat complexity

At mid-season in Laguna and Nueva Ecija, $\delta^{15}\text{N}$ values of plant- and leafhoppers closely matched the values of rice, indicating well-established herbivore populations feeding on rice phloem sap (Heong et al. 1992; Dale 1994). Fertilized rice plants provide high-quality, fitness-increasing food to plant- and leafhoppers, with short reproductive cycles enabling new generations of hoppers to feed exclusively on rice (Dyck et al. 1979; Lu and Heong 2009). This pattern was not observed in Ifugao, where *Sogatella furcifera* and *Nephotettix virescens* were depleted in $\delta^{15}\text{N}$ by 2.2 and 3.3‰ compared to rice, respectively, pointing to alternative host plant use. Colder mean temperatures, as in mountainous Ifugao, retard egg and larval development (Chapman 1998), resulting in a slower colonization of rice-paddies by plant- and leafhoppers. This manifests in isotope signatures of alternative host plants at a later date compared to regions with warmer climates (Schoenly et al. 2010; Chapter 2).

$\delta^{13}\text{C}$ values of plant- and leafhoppers increased from Laguna to Nueva Ecija to Ifugao. Connectivity between rice paddies and the shape complexity of fields within 200 m of the focal field significantly impacted the $\delta^{13}\text{C}$ values of plant- and leafhoppers (Chapter 3). With rice

being by far the most important food resource for plant- and leafhoppers in all three regions, slight differences between $\delta^{13}\text{C}$ values of rice and herbivores and large differences in $\delta^{15}\text{N}$ emphasize the importance of non-rice host plants in Ifugao.

Mountainous cropping regions have the highest plant species richness in semi-natural habitats, such as bund or levees surrounding fields (Fried et al. 2018). These refuges provide alternative non-rice food resources during fallow periods when rice is scarce, altering $\delta^{13}\text{C}$ values (Bambaradeniya and Edirisinghe 2008; Gurr et al. 2011; Chapter 2). This effect was especially pronounced in Ifugao, where traditional upland rice terraces have many interconnected bunds. Complex shapes of the rice-paddies have the same effect: the increased perimeter-to-area ratio leads to longer bunds accommodating more plant species that herbivores can feed on. Non-crop plants on bunds emit complex plant volatiles (Randlkofer et al. 2010), attracting herbivores and potentially diverting them from rice changing $\delta^{13}\text{C}$ values of species with differing diet width, such as *Nephotettix* and *Sogatella* (Dale 1994; Caton et al. 2010).

Spiders in rice-paddy ecosystems of different habitat complexity

$\delta^{13}\text{C}$ values of spiders differed significantly between regions, indicating a higher predation on aquatic midges in the lowland region Laguna and the highland region Ifugao, whereas in Nueva Ecija spiders preferred terrestrial plant- and leafhoppers. Aquatic-derived prey such as midges comprises the majority of spider nutrition across various biotopes (Sanzone et al. 2003; Gratton et al. 2008; Hambäck et al. 2016). Nonetheless, terrestrial herbivore prey also contributes profoundly to the diet of spiders (Heong et al. 1991b, 1992; Chapter 2). Maintaining complete inundation of paddies is more difficult in bigger fields, like in Nueva Ecija, resulting in less aquatic habitat and an accordingly low availability of aquatic prey. *T.*

javana builds webs above heights of one meter in tall grasses including rice, thus capturing midges more efficiently (Butt and Tahir 2010). General low prey availability in PH2 may have led to more intraguild predation, which is reflected in lower $\delta^{13}\text{C}$ values (Wise 2006).

Here, we also see the effect of increased plant species richness in mountainous landscapes like Ifugao compared to other rice cropping regions (Fried et al. 2017, 2018). Increased vegetation complexity and low management intensity, as is typical of Ifugao, leads to a higher diversity of web-building spiders (Diehl et al. 2013). Together, these factors lead to systematic differences between diets of spiders with different prey-capture strategies.

Hunting strategies determine spider nutrition and exploitation of aquatic and terrestrial resources (Wimp et al. 2013). Web-building spiders in rice-paddies have a wider diet breadth compared to cursorial hunters, practicing resource partitioning by time, strata and microhabitat (Uetz et al. 1978, 1999; Butt and Tahir 2010). Under the passive hunting strategy, web-builders only relocate their web and alter their diets when prey is scarce or unsuitable (Olive 1982). This results in the wide $\delta^{13}\text{C}$ ranges and higher fluctuations in contributions of plant-and leafhoppers and midges observed in this study.

On the other hand, $\delta^{13}\text{C}$ values of active hunting wolf spiders, and to a lesser degree, dwarf spiders, indicate a narrower diet breadth and smaller ranges in relative hopper and midge contributions because these taxa are selective hunters which actively choose their prey (Chapter 3). Wolf spiders preyed more on terrestrial herbivores in the simpler landscape of Nueva Ecija, but consumed aquatic detritivores in the more complex landscapes of Laguna and Ifugao (Chapter 3).

This finding confirms earlier results (Öberg 2007; Öberg et al. 2007) pointing to field margins, edges and bunds as the primary hunting grounds of *P. pseudoannulata* in landscapes like

Nueva Ecija, although this species is also known for hunting on the water surface (Ishijima et al. 2004). Since plant- and leafhoppers are considered low-quality prey (Sigsgaard 2000), the preference of *P. pseudoannulata* in Nueva Ecija may indicate scarcity of alternative midge prey.

Both $\delta^{13}\text{C}$ analysis and mixing models confirmed a significant impact of diversity and number of habitat patches within a 300 m radius, field-shape complexity and connectivity of bunds on the diets of different spider species (Chapter 3). All of these metrics reflect the degree to which non-crop habitats are available and accessible to both spiders and their prey. As discussed above and demonstrated by the shifting abundances found in Chapter 2, seminatural habitats function as refugia during harsh within-field conditions such as field preparation, early rice growth stages and harvest, from which predators and prey can recolonize rice-paddies when conditions improve (Rand et al. 2006; Schmidt et al. 2008; Tsutsui et al. 2016).

Due to their good dispersal abilities, spiders benefit from increased prey species richness at large spatial scales (Symondson et al. 2002; Tscharntke et al. 2005; Marja and Tscharntke 2022), as was underlined by greater abundances of wolf spiders and long-jawed spiders near ditches and forest areas in Japanese rice-paddies (Baba and Tanaka 2016; Baba et al. 2018, 2019). Complex field shapes increase the perimeter-to-area ratio and are associated with smaller field sizes, both of which increase the amount of semi-natural habitat available to agrobiont arthropods, with species-dependent consequences according to functional traits such as dispersal mode, body size and hunting strategy (Rusch et al. 2015; Gallé et al. 2018, 2020). The degree of interconnectedness of fields and semi-natural habitats combined with their spatial arrangement also affects spider abundance and diets (Haan et al. 2020), while increasing patch numbers can increase biological control via heightened predator activity (Bianchi et al. 2006).

Recommendations to strengthen biological control by spiders

Together, the two studies presented in this thesis highlight the necessity of managing agricultural landscapes to support spider populations at all points in the rice cropping cycle. Application of insecticides should be avoided whenever possible, since they kill predators and pests indiscriminately and disrupt food webs and biological control, ultimately resulting in pest resurgence and reoccurring outbreaks. Alternative prey out of the aquatic system, such as gnats and midges, is of paramount importance to foster spider populations early in the rice growth phase and enhance biological control.

Both enhancing alternative prey and providing refuges for spiders can be achieved through simple ecological engineering approaches. Whenever possible, crop residue should remain in the field or be returned after use as animal bedding; additional mulch should be applied to increase populations of aquatic detritivores which serve spiders as alternative prey in the early season before the arrival of terrestrial herbivores. Farmers can increase structural habitat complexity by cultivating a variety of crops and increasing local plant species richness, e.g. by planting flower strips on bunds and field margins. Both of these practices benefit spiders and other predators by providing alternative prey and refuge during harsh within-field conditions, such as field preparation or harvest. Slashing weeds, instead of using herbicides, and positioning weed bundles near or on the field makes the plants unattractive for plant- and leafhoppers but serves as refuge for spiders.

Conclusion

This thesis has improved our understanding of rice-associated food webs and, for the first time, applies stable isotope analysis to reveal detailed dietary dynamics during the rice cropping cycle in the tropics. It provides evidence of the scales at which landscape factors

influence diversity of a key predator, the biocontrol target, and an important alternative prey group. These results can inform management practices at local and landscape levels to foster more sustainable agro-ecosystems.

Spiders consume insects emerging from the aquatic system in the early cropping season before gradually shifting to terrestrial prey later in the season, reflecting changing prey availability. The effect is particularly strong in fields within heterogeneous landscapes. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of spiders follow those of aquatic detritivores early in the cropping cycle while converging toward values of terrestrial herbivores, indicating an increasing reliance on plant- and leaf-hoppers as the cropping season progresses (Chapter 2).

Rice-paddy spiders are sustained by three different carbon pools. In the early season they rely predominantly on carbon fixed by algae of the water body of rice fields, which is incorporated via gnats and midges. Later they mainly rely on carbon from previous growing cycles, incorporated via the next generation of gnats and midges, and finally carbon from the current cropping cycle, incorporated via planthoppers and leafhoppers (Chapter 2).

Differences in the patterns of spider and prey resource uses between the three cropping regions are mediated by management practices and landscape factors, rather than associated with highland or lowland regions. Spiders in Laguna rely more on aquatic-derived carbon from algae-feeding midges, whereas terrestrial-derived carbon is more prevalent in Nueva Ecija and Ifugao. High intraspecific variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values between cropping regions (Chapter 3) underline the fact that prey selection by spiders is highly dependent on species, hunting strategy and prey availability. Therefore, a diverse spider community that partitions prey and habitat resources can be an effective antagonist against a multitude of insect pest species.

Increased plant diversity provided by semi-natural habitats, such as gardens, grassland and forest connected by bunds, function as refugia for spiders and plant- and leafhoppers. Spiders, particularly cursorial species, move quickly between refugia and rice fields. Later, when plant- and leafhoppers colonize rice-paddies, the proportion of terrestrial prey consumed by spiders increases, most notably in heterogeneous landscapes and regions with higher landscape complexity (Chapters 2, 3). The number and variety of habitat patches both significantly affect prey availability and spider nutrition (Chapters 2, 3), with knock-on effects for biological control. Independent of time or region, alternative prey out of the aquatic system is paramount to fostering spider populations and enhancing biological control (Chapter 2, 3).

The unique aquatic and terrestrial compartments of the rice-ecosystem are intricately bound together. This provides the great opportunity, more than in any other agro-ecosystem, to achieve effective biological control through ecological engineering. The results of this thesis suggest that ecological engineering approaches can foster spider diversity and abundance, important factors for effective biological control and increased sustainability of rice and other agro-ecosystems.

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Appendix A

Table 3: Generalized linear mixed effects model: effect of *date* and *structure* on abundance of gnats/midges.

	DF	F	p
date	2	29.5	<0.001
structure	1	0.0	0.65
date x structure	2	43.1	<0.001

Table 4: Likelihood ratio test comparing models of gnat/midge abundance with and without random effects.

	DF	AIC	BIC	Log-Likelihood	deviance	Chi ²	p
without random effects	7	13210	13219	-6599.1	13198.1		
with random effects	9	637	651	-309.6	619.3	0	<0.001

Table 5: Generalized linear mixed effects model: effect of *date* and *structure* on abundance of plant-/leafhoppers.

	DF	F	p
date	2	100.9	<0.001
structure	1	0.9	0.54
date x structure	2	4.4	<0.001

Table 6: Likelihood ratio test comparing models of plant-/leafhoppers abundance with and without random effects.

	DF	AIC	BIC	Log-Likelihood	deviance	Chi ²	p
without random effects	3	1376	1381	-685.4	1370.9		
with random effects	5	333	341	-161.9	323.8	1047.1	<0.001

Table 7: Generalized linear mixed effects model: effect of *date* on abundance of spiders.

	DF	F	p
date	2	286.4	0.001

Table 8: Likelihood ratio test comparing models of spider abundance with and without random effects.

	D F	AIC	BIC	Log- Likelihood	devianc e	Chi ²	p
without random effects	3	1376	1381	-685.4	1370.9		
with random effects	5	333	341	-161.9	323.8	1047. 1	<0.00 1

Table 9: Linear mixed-effects mode: effect of *date* and *species* on $\delta^{13}\text{C}$ values of gnats-/midges.

	numDF	denDF	F	p
date	2	55	35764	<.0001
species	1	55	< 0.1	0.0776
date x species	2	55	3257	0.0461

Table 10: Comparison of models of $\delta^{13}\text{C}$ values of gnats/midges with and without random effects.

	DF	AIC	BIC	Log-Likelihood	L. Ratio	p
without random effects	7	267	283	-126.9		
with random effects	9	266	287	-124.2	5.254629	0.0723

Table 11: Linear mixed-effects mode: effect of *date*, *structure* and *species* on $\delta^{13}\text{C}$ values of plant-/leafhoppers.

	numDF	denDF	F	p
date	2	122	8.8	<.0003
structure	1	2	0.2	0,698
species	5	122	24.0	<.0001
date x structure	2	122	4.1	0.0189

Table 12: Comparison of models of $\delta^{13}\text{C}$ values of plant-/leafhoppers with and without random effects.

	DF	AIC	BIC	Log- Likelihood	L. Ratio	p
without random effects	12	394	429	-185.3		
with random effects	14	367	407	-169.7	31.1	0.0001

Table 13: Linear mixed-effects mode: effect of *date*, *structure* and *species* on $\delta^{13}\text{C}$ values of spiders.

	numDF	denDF	F	p
date	2	109	54.8	<.0001
structure	1	2	0.6	0.493
species	6	109	5.4	0.0001
date x structure	2	109	4.9	0.0086

Table 14: Comparison of models of $\delta^{13}\text{C}$ values of spiders with and without random effects.

	DF	AIC	BIC	Log-Likelihood	L. Ratio	p
without random effects	13	485	521	-229.9		
with random effects	15	471	512	-220.5	18.8	0.0001

Table 15: Area, elevation and ascribed landscape properties of investigated field sites.

LEGATO-field site	area [m ²]	elevation [m above sea level]	rice- hetero- geneous	rice- homo- geneous
PH1-R3	820	275	+	-
PH1-R4	960	275	-	+
PH1-R9	2400	25	+	-
PH1-R14	875	25	-	+

Appendix B

Table 2: Carbon and nitrogen stable isotope ratios (means \pm SD) and number of samples (n) of arthropods and rice pooled for structured and unstructured fields two, four and six weeks after transplantation (WAT) during the rainy season 2012.

Taxa	$\delta^{13}\text{C}$ [‰]									$\delta^{15}\text{N}$ [‰]								
	2 WAT			4 WAT			6 WAT			2 WAT			4 WAT			6 WAT		
	Mean	\pm sd	n	Mean	\pm sd	n	Mean	\pm sd	n	Mean	\pm sd	n	Mean	\pm sd	n	Mean	\pm sd	n
Primary producer																		
<i>Oryza sativa</i>	-29.52	0.71	3	-29.67	0.13	3	-28.87	0.23	3	4.25	0.67	3	1.99	4.12	3	5.50	0.44	3
Aquatic polyphages																		
Ceratopogonidae, adult	-21.94	1.24	8	-22.64	1.56	4	-23.97	1.27	4	5.98	1.09	8	6.23	1.41	4	3.80	2.12	4
Ceratopogonidae, larval	-21.77	2.37	10	-20.78	1.86	12	-23.34	3.00	12	4.56	1.36	10	3.47	1.44	12	3.67	2.15	12
Chironomidae, adult	-20.52	1.41	11	-22.49	1.91	10	-24.15	1.32	6	6.78	1.28	11	4.60	1.35	10	6.49	0.70	6
Chironomidae, larval	-22.36	2.31	10	-21.63	2.12	12	-24.50	1.64	11	6.47	0.97	10	4.56	1.24	12	5.39	1.62	11
Herbivores																		
Cicadellidae, nymphs	-27.43	1.56	5	-26.09	6.57	11	-27.93	1.10	11	4.59	1.27	5	2.20	1.27	11	4.08	2.03	11
<i>Nephotettix nigropictus</i>	-26.84	2.19	2	-27.04	0.78	10	-25.60	2.95	8	4.16	0.84	2	4.56	1.90	10	4.86	1.12	8
<i>Nephotettix virescens</i>	-29.24	0.44	3	-28.78	0.73	10	-28.64	0.79	11	5.57	1.40	3	3.53	2.70	10	4.25	1.16	11
<i>Recilia dorsalis</i>	-28.57	-	1	-29.04	0.48	8	-29.20	0.80	12	0.56	-	1	4.19	1.87	8	3.60	1.49	12
Delphacidae, nymphs	-28.28	0.77	7	-28.45	0.67	12	-29.12	0.93	8	6.55	0.73	7	3.13	2.36	12	4.08	1.33	8
<i>Sogatella furcifera</i>	-25.82	5.09	5	-29.25	0.67	11	-27.97	3.17	12	3.48	2.94	5	4.13	1.44	11	4.04	1.28	12
Predators																		
<i>Atypena adelinae</i>	-21.38	1.75	2	-23.40	1.11	12	-24.81	1.44	10	8.64	1.04	2	6.68	0.80	12	7.20	0.94	10
<i>Araneus inustus</i>	-20.02	1.56	6	-22.38	2.44	8	-22.70	2.28	5	7.72	0.61	6	7.44	1.09	8	6.77	0.63	5
<i>Dyschiriognatha hawigtenera</i>	-	-	-	-23.25	0.81	5	-24.68	1.92	7	-	-	-	6.28	0.72	5	6.80	1.20	7
<i>Pardosa pseudoannulata</i>	-	-	-	-22.11	1.54	9	-23.17	1.77	7	-	-	-	8.04	1.61	9	7.00	1.28	7

<i>Tetragnatha javana</i>	-20.08	0.95	5	-22.33	1.29	10	-22.68	1.84	9	7.96	1.27	5	6.50	0.59	10	7.39	0.93	9
<i>Tetragnatha maxillosa</i>	-18.33	0.67	3	-22.24	1.83	2	-23.46	1.29	5	7.99	0.06	3	7.56	0.97	2	7.52	0.92	5
<i>Tetragnatha virescens</i>	-20.05	1.03	6	-21.85	1.53	10	-23.05	2.03	10	7.75	1.54	6	6.98	0.93	10	6.49	1.29	10

Appendix C

Table 2: Linear mixed-effects model: effect of *region* on $\delta^{13}\text{C}$ values of midges.

	numDF	denDF	F	p
region	2	9	4.4	0.0476

Table 3: Linear mixed-effects model: effect of *region*, *species* and *FRAC* at 200 m distance on $\delta^{13}\text{C}$ values of plant-/leafhoppers.

	numDF	denDF	F	p
region	2	8	7.4	0.0151
species	1	8	0.3	0.6087
<i>FRAC200</i>	1	37	2.0	0.1626
<i>FRAC200</i> x species	1	37	8.9	0.0051

Table 4: Linear mixed-effects model: effect of *region*, *species* and *COH* at 300 m distance on $\delta^{13}\text{C}$ values of plant-/leafhoppers.

	numDF	denDF	F	p
region	2	8	9.9	0.0070
species	1	8	3.3	0.1054
<i>COH300</i>	1	37	1.8	0.1832
<i>COH300</i> x species	1	37	8.9	0.0050

Table 5: Linear mixed-effects model: effect of *region*, *species* and *COH* at 200 m distance on $\delta^{13}\text{C}$ values of plant-/leafhoppers.

	numDF	denDF	F	p
region	2	8	8.6	0.0101
species	1	8	1.4	0.2738
<i>COH200</i>	1	37	1.7	0.2010
<i>COH200</i> x species	1	37	4.9	0.0322

Table 6: Linear mixed-effects model: effect of *region*, *species* and *FRAC* at 100 m distance on $\delta^{13}\text{C}$ values of spiders.

	numDF	denDF	F	p
region	2	8	5.1	0.0382
species	4	69	1.4	0.2478
<i>FRAC100</i>	1	8	0.1	0.7481
region x species	8	69	3.4	0.0025
species x <i>FRAC100</i>	4	69	2.8	0.0345

Table 7: Linear mixed-effects model: effect of *region*, *species* and *SHDI* at 300 m distance on $\delta^{13}\text{C}$ values of spiders.

	numDF	denDF	F	p
region	2	8	9.2	0.0085
species	4	69	1.4	0.2570
<i>SHDI300</i>	1	8	10.8	0.0112
region x species	8	69	3.4	0.0025
species x <i>SHDI300</i>	4	69	3.5	0.0115

Table 8: Linear mixed-effects model: effect of *region*, *species* and *SHDI* at 200 m distance on $\delta^{13}\text{C}$ values of spiders.

	numDF	denDF	F	p
region	2	8	9.4	0.0079
species	4	69	1.4	0.2536
<i>SHDI200</i>	1	8	10.7	0.0114
region x species	8	69	3.5	0.002
species x <i>SHDI200</i>	4	69	3.7	0.0083

Table 9: Linear mixed-effects model: effect of *region*, *species* and *SHDI* at 100 m distance on $\delta^{13}\text{C}$ values of spiders.

	numDF	denDF	F	p
region	2	8	7.0	0.0175
species	4	69	1.4	0.2406
<i>SHDI100</i>	1	8	5.9	0.0412
region x species	8	69	3.5	0.002
species x <i>SHDI100</i>	4	69	3.6	0.0101

Table 10: Linear mixed-effects model: effect of *region*, on $\delta^{13}\text{C}$ values of rice.

	numDF	denDF	F	p
region	2	9	0.7	0.5346

Table 11: Linear mixed-effects model: effect of *region*, on prey contributions to spiders.

	numDF	denDF	F	p
region	2	9	0.5	0.656
species	3	16	0.8	0.5379
region x species	6	16	4.8	0.0056

Table 12: Table 10: Linear mixed-effects model: effect of *NP300*, on prey contributions to spiders.

	numDF	denDF	F	p
region	2	8	0.6	0.5509
species	3	16	0.8	0.5339
<i>NP300</i>	1	8	6.7	0.0319
<i>NP300</i> x species	6	16	4.6	0.0067

Table 13: Table 10: Linear mixed-effects model: effect of *COH100*, on prey contributions to spiders.

	numDF	denDF	F	p
region	2	8	0.6	0.5606
species	3	16	0.8	0.5353
<i>COH100</i>	1	8	5.9	0.0401
<i>COH100</i> x species	6	16	4.6	0.0070

Appendix D

Table 14: Carbon and nitrogen stable isotope ratios (means \pm SD) and number of samples (n) of arthropods and rice pooled for fields in regions Laguna (PH1), Nueva Ecija (PH2) and Ifugao (PH3) during the dry season 2013.

Taxa	$\delta^{13}\text{C}$ [‰]									$\delta^{15}\text{N}$ [‰]								
	PH1			PH2			PH3			PH1			PH2			PH3		
	Mean	\pm sd	n	Mean	\pm sd	n	Mea	\pm sd	n	Mea	\pm sd	n	Mean	\pm sd	n	Mea	\pm sd	n
Primary producer																		
<i>Oryza sativa</i>	-	1.1	1		0.7	1	-	0.3	1		2.7	1		0.8	1		2.6	1
	29.52	0	2	-29.21	8	2	28.79	7	2	5.57	5	2	3.61	8	2	5.46	1	2
Aquatic polyphages																		
Chironomidae, adult	-	0.8	1		1.5	1	-	1.2	1		0.9	1		1.4	1		1.1	1
	24.96	3	2	-25.23	0	6	23.83	5	2	7.54	7	2	5.31	3	6	4.45	3	2
Chironomidae, larval	-	1.7	1		2.1	1	-	2.6			1.5	1		4.2	1		2.8	
	24.20	1	2	-26.93	7	0	26.14	0	9	7.02	9	2	6.15	8	0	3.61	3	9
Herbivores																		
<i>Nephotettix nigropictus</i>					0.5									0.3				
	-	-	-	-26.95	7	2	-	-	-	-	-	-	3.15	1	2	-	-	-
<i>Nephotettix virescens</i>	-	0.6	1		0.8	1	-	1.1	1		1.3	1		1.3	1		1.0	1
	28.92	9	2	-28.07	8	3	28.06	5	1	5.25	8	2	2.87	3	3	2,20	2	1
<i>Sogatella furcifera</i>	-	1.7	1		0.8	1	-	1.1	1		1.3	1		1.7	1		2.1	1
	28.79	7	2	-28.58	7	7	27.64	3	2	5.34	3	2	3.61	5	7	3.72	7	2

Predators

	-	1.4	1		0.3					0.9	1		0.9					
<i>Atypena adelinae</i>	24.77	0	3	-24.11	2	4	-	-	-	8.48	8	3	6.87	4	4	-	-	-
	-	1.4	1		0.8	1	-	1.1		0.8	1		1.1	1		1.0		
<i>Araneus inustus</i>	23.80	0	3	-23.94	9	0	21.22	6	2	7.74	5	3	5.97	9	0	7.10	5	2
	-	1.6	1		1.0		-	0.5		1.1	1		1.8			0.0		
<i>Pardosa pseudoannulata</i>	23.44	8	1	-24.95	1	5	23.95	6	3	8.85	7	1	5.94	4	5	7.92	9	3
	-	1.4	1		2.0		-	2.0	1	0.6	1		1.2			1.0	1	
<i>Tetragnatha javana</i>	22.44	0	1	-25.56	4	2	22.80	2	2	8.29	5	1	6.54	1	2	5.04	6	2
	-																	
<i>Tetragnatha mandibulata</i>	23.53	-	1	-23.54	-	1	-	-	-	8.66	-	1	7.57	-	1	-	-	-
	-	0.7					-	1.7	1	0.6						1.2	1	
<i>Tetragnatha maxillosa</i>	22.04	6	8	-	-	-	24.09	4	2	8.40	6	8	-	-	-	5.04	1	2
					0.4								0.0					
<i>Tetragnatha nitens</i>	-	-	-	-24.22	3	2	-	-	-	-	-	-	4.43	2	2	-	-	-
<i>Tetragnatha vermiformis</i>	-	-	-	-24.66	-	1	-	-	-	-	-	-	6.73	-	1	-	-	-
	-	1.3			1.6		-	1.2	1	0.6			1.2			1.1	1	
<i>Tetragnatha virescens</i>	22.50	6	9	-25.74	3	7	23.17	9	1	8.25	9	9	5.53	9	7	5.00	8	1

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N. R., 2022

Curriculum vitae

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Work Experience

- 30.01.2020 Publication „Spiders in rice-paddy ecosystems shift from aquatic to terrestrial prey and use carbon pools of different origin” in journal *Oecologia*, Springer Verlag
<http://link.springer.com/article/10.1007/s00442-020-04601-3>
- 2018 Participation „Introduction to GIS“ at the Faculty of Geography University of Göttingen
- 2015-19 leading excursion groups of students within „zoologischen Bestimmungsübungen“ of the Animal Ecology working group, University of Göttingen
- 09.2015 Talk at the annual meeting of Gesellschaft für Ökologie (GfÖ), topic „Do spiders in Philippine rice fields prefer aquatic over terrestrial prey?“
- 09.2014 Talk at the annual meeting of Gesellschaft für Ökologie (GfÖ), topic „The role of aquatic and terrestrial resources for generalist predators and pest control in rice fields“

- 2012/ 2013 Sampling expedition in Luzon, Philippines within the framework of the LEGATO-Project in cooperation with International Rice Research Institute (IRRI) und PhilRice
- since 01.03.2012 PhD student within the framework of the LEGATO-Project, working group of Prof. Dr. Scheu, Department of Animal Ecology, Georg-August-University Göttingen
- 02.-12. 2011 research associate (wissenschaftlicher Mitarbeiter) at Zentrum für Philosophie und Grundlagen der Wissenschaft, working group of Herr Prof. Dr. Voland
- 05.- 11. 2010 research assistant, working group of Prof. Dr. Wolters, Department of Animal Ecology, Justus-Liebig-University Gießen
- poster presentation based on diploma thesis data on the annual GfÖ-conference 2010

College Education

- 10.2003- 05.2010 Studies in Biology at Justus-Liebig-University Gießen graduated with diploma degree, topic of diploma thesis: „Influence of greenland-management and geographical position of spider communities in the DFG-biodiversity exploratories“, (original: „Einfluss der Grünland-Bewirtschaftung und der geographischen Lage auf die Spinnengemeinschaften in den DFG-Biodiversitätsexploratorien“)

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- 08.1993 – 05.2002 Dietrich-Bonhoeffer-Gymnasium Bergisch Gladbach, graduated with Abitur

List of publications

Peer reviewed journal publications

Radermacher N, Hartke TR, Villareal S, Scheu S (2020) Spiders in rice-paddy ecosystems shift from aquatic to terrestrial prey and use carbon pools of different origin. *Oecologia* 192:801–812. doi: 10.1007/s00442-020-04601-3

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Planned publications

Radermacher N, Hartke TR, Dominik C, Scheu S (2022) Variation in the diet of spiders in rice paddy ecosystems of different landscape complexity depends on species identity and hunting strategy