Intensification of paddy cultivation in relation to changing agrobiodiversity patterns and social-ecological processes in South India

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Introduction

INTRODUCTION

Paddy (*Oriza sativa*) is an annual grass, probably domesticated roughly 9,000 years ago in several Asian regions independently (Khush 1997). Today it is the most widely distributed crop in the world and one of the world's most important food crop. Adaptable to a large range of environmental conditions paddy is grown in different cultivation systems. Four major rice ecosystems are distinguished, namely irrigated, rainfed lowland, upland and floodprone rice (Khush 1997). During the centuries countless different local varieties have been developed by farmer selection to meet various environmental conditions and cultural needs; for instance in India an estimated 25,000 varieties are stored in gene banks (Khush 1997; Kumar et al. 2010) Subrahamanian et al. 2007).

Starting in the mid-1960s, traditional paddy cultivation was drastically transformed by the Green Revolution, the greatest intervention in rice cultivation in Asia, which aimed at a considerable increase in rice production to meet the requirements of the rapidly growing population. This increase was accomplished by increasing paddy cultivation area on the one hand and by raising production per unit cultivated land on the other. The latter was achieved by the introduction of high yielding varieties which produce less foliage but more ears, by double or triple cropping, ensured due to reduced duration of high yielding varieties, by irrigation, the use of machinery and by the introduction of chemical fertiliser and pesticides (Settle et al. 1996; Pandey et al. 2010; Horgan & Crisol 2013). This intensification had led to an increase in yield, yet with severe environmental consequences. Increased fertilisation not only enhances crop growth but also can be a reason for the build up of insect pest populations due to increased nutritious value of the crop (Lu & Heong 2009; Horgan & Crisol 2013) or enhanced weed growth (Major et al. 2005). The application of insecticides often not only eliminates the targeted pest species but also beneficial natural enemies which in turn can lead to outbreaks of secondary pests (Settle et al. 1996; Tilman et al. 2001; Lu et al. 2014).

Agricultural fields, especially annual crops such as paddy, are frequently disturbed by several management practices and therefore floral and faunal diversity in such fields depends on the colonisation by plants and animals from source habitats in the surrounding landscapes. Those source habitats can be manifold, forests, hedgerows, flowerstrips along the fields, agroforests, or homegarden polycultures for instance (Bianchi et al. 2006, Rand et al. 2006, Batáry et al. 2011). However, landscape wide land-use change by expansion of agricultural land, by establishing monocultures and changes in cultivated crop types is a global phenomenon (Matson 1997; Tilman et al. 2001). Since the reduction of natural or semi-natural habitats not only leads to a decline of biodiversity but also to the loss ecosystem services associated with biodiversity, agricultural transition on landscape scale became of increasing interest (Altieri 1999; Wilby & Thomas 2002; Tscharntke et al. 2005; Bianchi et al. 2006; Amano et al. 2011).

These agricultural transitions also affect small-scale and subsistence farming in rural South India, where rice is one of the major food crop and paddy cultivation often closely linked to cultural and religious practices.

STUDY REGION: WAYANAD DISTRICT IN KERALA, SOUTH INDIA

Wayanad district, located in the north of Kerala State, South India (Fig. 1) is part of the Western Ghats, a mountain range stretching from north to south along the Indian west coast. The Western Ghats are a bio-cultural diversity hotspot (Pretty et al. 2009; Brosius & Hitchner 2010) and has recently become one of the UNESCO Natural World Heritage sites (UNESCO World Heritage Centre 1992-2013 2012). Wayanad is an undulating plateau, abruptly descending in the west to Kerala plains but merging imperceptibly with the Mysore plateau in the east. The elevation ranges from 700 to 2100 meters above MSL. The climate is tropical with an annual rainfall of 2,322 mm and a mean temperature range of 18 °C to 29 °C.

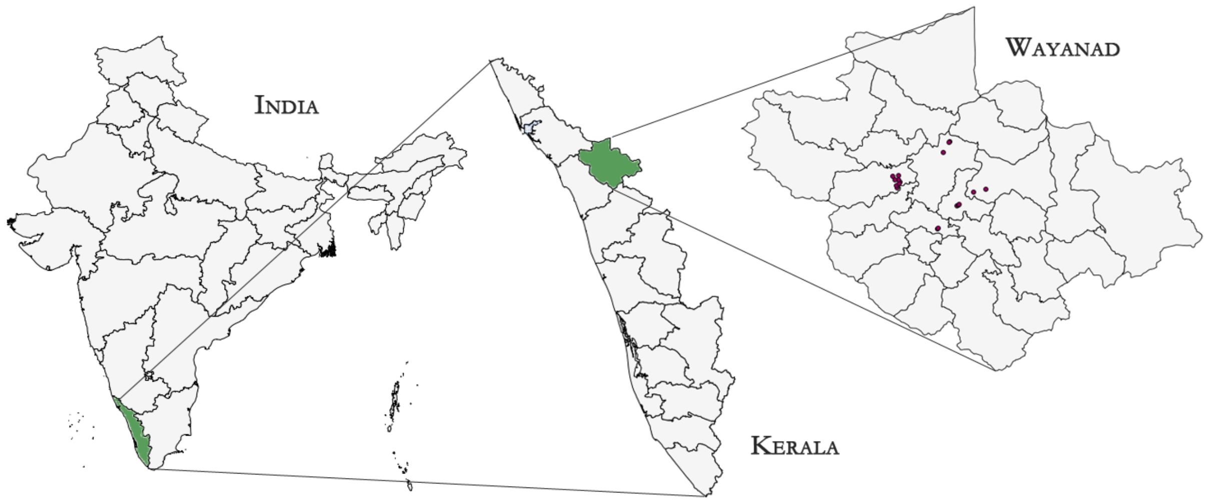

Figure 1: Wayanad district of Kerala State in South India.

The District covers an area of 212,560 ha which was once mainly covered by forest. However, large-scale deforestation started in the 19th century when British authorities established the production of tea, coffee and cardamom. Related migration of agricultural labourers to Wayanad further changed agriculture but also cultural traditions (George & Krishnaprasad 2006; Suma 2014). Today approximately 97 % of the area is under agricultural use, mostly subsistence farming and small holder plantations (Santhoshkumar & Ichikawa 2010). Located on the hill-tops are the farm houses surrounded by homegarden polycultures containing fruit and timber trees, coffee, spices, coconut palms, arecanut, vegetables etc. that supplied the households with food. In the plains, flooded during the monsoon season, different varieties of paddy are cultivated, predominantly during the Nancha season which starts with the southwest monsoon in July and ends with harvest in December (Fig. 2) (Kumar et al. 2010). The influences of the Green Revolution also reached, with some delay and probably less powerful, such remote areas as Wayanad and are still ongoing. Furthermore, by the end of the 1990s the commercialisation of agriculture and the introduction of cash crops such as banana, arecanut, ginger and turmeric changed land-use patterns in Wayanad. Cash crops are less labour demanding and by far more profitable than paddy cultivation (George & Krishnaprasad 2006; personal communication with farmers). This development resulted in a decline in paddy area in Wayanad from 30,000 ha in 1980-81 to 8,995 ha in 2011-12 (GOI 2013). Furthermore, this commercialisation led to increasing conversion of homegarden area into rubber or coffee plantations. Moreover labour migration, education, and the public distribution system contribute to decreasing interest in agriculture in general and in paddy cultivation in particular. Despite all this, paddy cultivation is still continued by many farmers and recently promoted by the local government. According to one farmer: "there will always be paddy cultivated in Wayanad".

Figure 2: Agricultural landscape in Wayanad.

Wayanad is notable for its large indigenous population, known as Adivasi, an umbrella term for indigenous or tribal population groups in India (Rath 2006). Wayanad has the highest proportion (17.43 %) of Adivasi inhabitants in Kerala (1.14 %) but also the highest level of poverty amongst Adivasis (Chathukulam & John 2006; Münster and Vishnudas, 2012). The Kerala Government distinguishes between twenty Adivasi groups in Wayanad. They can be broadly classified into farming communities, landless agricultural labourers, artisan communities and hunter-gatherer communities (Nair 1911; Indian Institute of Management 2006). For many Adivasi paddy cultivation is especially closely linked with their livelihood strategies, their culture and religion and therefore external challenges such as the agricultural crisis in India (Lerche 2011) and the agricultural transitions described above affect them in particular (Kurup 2010; Kulirani 2011). Furthermore, changing family structures and the reorganization of labour lead to shifts in their social organisation (Kunze & Momsen 2015).

Figure 3: Kurichya settlement in Wayanad.

This is the context were the BioDIVA project, in which this thesis was embedded in, related to. BioDIVA was part of the social-ecological research programme by the BMBF (German Federal Ministry of Education and Research) and was organised in collaboration with the M.S. Swaminathan Research Foundation in India, an influential NGO concerning all matters of agriculture and conservation. The project had three main objectives: (1) the social organisation of agrobiodiversity, its management and transformation (2) the impacts of land-use change on income and labour and (3) the effects of land-use change on the paddy agrobiodiversity. Furthermore, BioDIVA followed a transdisciplinary approach by integrating farmers, local politicians and administration in the research process.

RESEARCH OBJECTIVES

The effects of land-use change and different agricultural practices have been studied in a range of different geographic regions and land-use contexts (e.g. Roschewitz et al. 2005; Tscharntke et al. 2005; Stenchly et al. 2012; Takada et al. 2012; Martin et al. 2013; Zulka et al. 2014). However, despite the seminal work of Settle et al. (1996) for instance, the impact of landscape-wide land-use change and intensified cultivation practices on weeds, pests and predators in paddy cultivation are so far little studied and understood. Furthermore, in the context of social-ecological research we met the challenges of integrating different disciplines and stakeholders in the research process (Pohl & Hirsch Hadorn 2008; Bergmann et al. 2010).

The thesis at hand addresses the following main research questions:

(1) How does landscape structure and local agricultural management affect weed, planthopper and spider communities in paddy fields?
(2) How do spider families and spider web types found in rice fields respond to prey availability, management practices and landscape components?
(3) How does land-use change shape the social-ecological transformation processes and agricultural practices of different indigenous communities?

CHAPTER OUTLINE

Chapter 1: Paddy weeds, pests and predators respond to agricultural intensification at local and landscape scales

This study investigates the response of paddy weeds, pests and predators to agricultural intensification on a local and landscape scale. For this, weeds, leaf- and planthoppers and spiders were collected in the 18 paddy fields that adjoined either homegarden polycultures or banana monocultures and were cultivated by applying low-intensity or high-intensity management. The results showed that adjacent banana monocultures enhanced weed and planthopper population. The abundance of planthoppers was positively related to the density of weedy grasses while spider population was mainly driven by the availability of prey. Increased fertiliser application had an indirect positive effect on spiders through increased prey abundance and weed richness. Decreasing spider abundance and richness from the field edges towards the bund indicates influences of adjacent habitat on paddy field colonisation. The findings of this study suggest that paddy cultivation in Wayanad should consider the identity of adjacent habitat and weeds (monocots vs dicots) but also the amount of applied fertilisers to maintain a balanced agroecosystem.

Chapter 2: Spider families and spider webs in Indian rice fields – an assessment of local and landscape effects

This chapter particularly focuses on spider community and addressed the question how the most abundant spider families and spider web types respond to prey availability, management practices and landscape components. The analysis highlighted that the major determining factor for overall spider and web abundance is the prey availability, hence the spider community in these paddy fields is driven by bottom up effects. A closer look at different families and web types revealed differences within this general pattern. The results further showed that spider web sampling can be a useful addition to spider sampling. Missing effect of management practices suggest that intensification in this area not yet reached a critical point. Furthermore, huge numbers of tetragnathid webs, which are easy to observe in the field, can be an indicator for the farmers to check their fields for possibly harmful infestation with rice pests.

Chapter 3: The social-ecological web: A bridging concept for transdisciplinary research

The focus of this study was on a social-ecological approach to assess the ecological knowledge and agricultural practices as well as the multiple meanings of social-ecological transformation processes using the example of the three major Adivasi communities in Wayanad. Central to this qualitative study was the development of a social-ecological web which is understood as a bridging concept that integrates knowledge from social and natural science. This method is a useful tool to illustrate and compare the different agrarian systems. The results revealed that land-use change and intensification causes different degrees of social-ecological transformation among the three indigenous communities.

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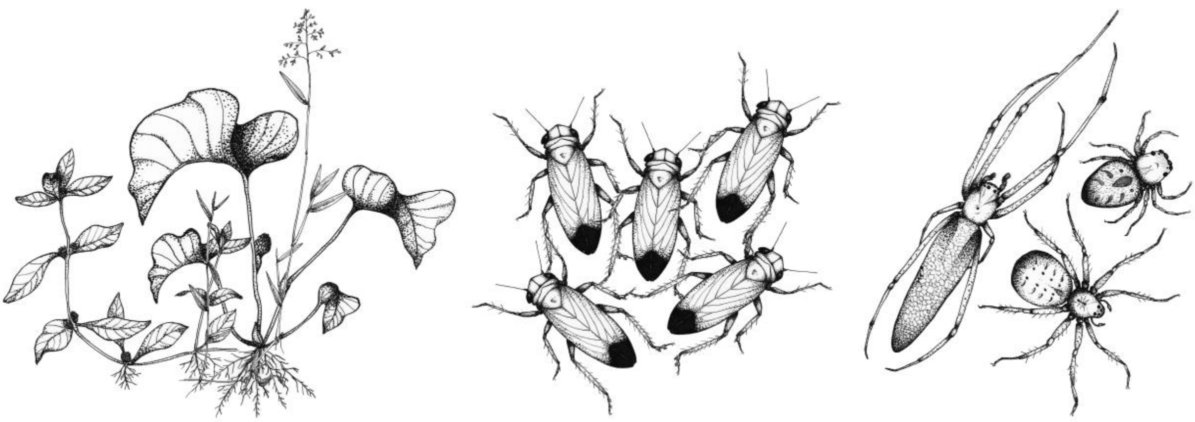
Chapter 1

PADDY WEEDS, PESTS AND PREDATORS RESPOND TO AGRICULTURAL INTENSIFICATION AT LOCAL AND LANDSCAPE SCALES



ABSTRACT

Land-use change and agricultural intensification are global phenomena that also affect small-scale and subsistence farming. In rural South India (Kerala: Wayanad district) paddy cultivation has a long tradition, but farming practices changed during the last decades. Paddy cultivation has become more intensified with the introduction of agrochemicals and high yielding varieties. Furthermore, paddy area is transformed for cash crop cultivation which is increasingly popular because of higher profitability compared to paddy. Nevertheless, many farmers still continue paddy cultivation. Therefore, this study aims at a better understanding of the impacts of landscape-wide land-use change and intensified cultivation practices on weeds, pests and predators in paddy cultivation, which are little studied so far. In 2011 and 2012 plants, planthoppers and spiders were collected in 18 paddy fields, cultivated by local farmers, applying either high-intensity or low-intensity management. Fields adjacent to homegarden polycultures and banana monocultures were selected to account for the current land-use change. Samples were taken in transects at the edge, the centre and the bund of the fields to consider possible edge effects. The results showed that adjacent banana monocultures enhanced the weed and planthopper population. Furthermore, the abundance of planthoppers was positively related to the density of weedy grasses but negatively affected by weed diversity (dominated by dicots). Spiders in contrast, benefited from weed diversity. However, their population was mainly driven by prey availability. Fertiliser application had an indirect positive effect on spiders through increased insect abundance and weed richness. Furthermore, spider abundance and richness decreased with increasing distance from the field edge, indicating influences of adjacent habitat on paddy field colonisation. The findings of this study suggest that paddy cultivation in Wayanad should consider the identity of adjacent habitat and weeds but also the amount of fertilisers applied to maintain a balanced agroecosystem.

Keywords: Rice, edge effect, land-use change, spiders, leaf- and planthoppers, plants

INTRODUCTION

Around the globe natural and agrarian landscapes are subject to agricultural intensification to meet the increasing and changing demands of the growing population for resources. This intensification takes place at two different scales. First, at landscape scale by the reduction of natural and semi-natural habitats to make room for the expansion of agricultural land, by establishing (large scale) monocultures and by changes in cultivated crop types (Tilman et al.

2001; Laurance 2010). Second, at local scale, intensification includes a shift in agronomic practices like increasing application of agrochemicals, use of heavy machinery, the cultivation of improved crop varieties and the reduction of genetic diversity (Matson 1997; Horgan & Crisol 2013). Reduction of natural or semi-natural habitats and simplification of landscape structure can negatively affect floral and faunal diversity and its associated ecosystem functions in agricultural fields due to reduced source or refuge habitats (Altieri 1999; Wilby & Thomas 2002; Bianchi et al. 2006; Martin et al. 2013). Intensified cultivation practices like increased fertilisation not only enhance crop growth but also can be a reason for the build up of insect pest populations due to increased nutrition value of the crop (Lu & Heong 2009; Horgan & Crisol 2013). The application of insecticides often not only eliminates the targeted pest species but also beneficial natural enemies and can lead to outbreaks of secondary pests (Settle et al. 1996; Tilman et al. 2001; Lu et al. 2014).

These agricultural transitions also affect small-scale and subsistence farming in the Tropics. In agricultural areas in Kerala, South India, where rice is a staple food and paddy cultivation has a very long tradition, those changes can be observed as well. Land-use change at landscape scale includes the transformation of forest and semi-natural habitats such as homegarden polycultures to plantations e.g. for coconut, rubber, tea, coffee, but also the transformation of paddy land into fields for cash crops such as bananas, arecanut, cassava, ginger, etc. (Kumar 2005; George & Krishnaprasad 2006; Suma 2014). At local scale, intensification of paddy fields implies a transition from traditional paddy cultivation without agrochemicals and a high number of farmer bred varieties towards management comprising limited number of improved rice varieties, application of chemical fertiliser and pesticides and mechanisation of agricultural practices (George & Krishnaprasad 2006; Kumar et al. 2010).

The effects of land-use change and different agricultural practices have been studied in a range of different geographic regions and land-use contexts (e.g. Tscharntke et al. 2005; Amano et al. 2011; Stenchly et al. 2012; Takada et al. 2012; Martin et al. 2013; Zulka et al. 2014) However, despite the seminal work of Settle et al. (1996) for instance, the impact of landscape-wide land-use change and intensified cultivation practices on weeds, pests and predators in paddy cultivation are so far little studied and understood.

Paddy fields, formed of two microhabitats, the cultivated patches and the earthen bunds surrounding them, harbour interacting plants and animals that may affect paddy cultivation in one or the other way. Spiders are important generalist predators in agriculture in general, and in paddy fields specificallys (Amano et al. 2011; Takada et al. 2012; Lou et al. 2013). Spiders are a highly efficient group of predators, because of diverse foraging strategies and activity patterns which makes them useful natural pest control agents in agricultural fields (Marc et al. 1999; Sunderland 1999; Foelix 2011).

In paddy cultivation areas leaf- and planthoppers (hereafter referred to as planthoppers) are a major insect pests, causing tremendous losses in cases of mass outbreaks (Settle et al. 1996; Wilby & Thomas 2002; Lu et al. 2014). Several studies report that spiders can effectively control leafhopper populations (e.g. Kiritani et al. 1972; Way & Heong 1994; Lou et al. 2013).

Farmers usually consider weeds in agricultural fields to be competitors of the crop. However, weeds may play a larger role in agroecosystems as they can represent an alternative food source or refuge habitat for both natural enemies and pests species (Schoenly et al. 1996; Nyffeler & Sunderland 2003; Bàrberi et al. 2010).

The aim of this study was to assess the effects of landscape structure and local agricultural management on spider, planthopper and weed communities in South Indian paddy fields. Therefore, we selected paddy fields neighbouring either homegarden polycultures or banana monocultures. Furthermore, the landscape complexity within a 500 m radius around each paddy field was taken into account. To account for changes in agronomic practices we differentiated between intensified and low-intensity paddy fields.

We hypothesised that:

(1) Spiders and weeds are positively affected by a diverse adjacent habitat such as homegarden polycultures and by a complex structured landscape in the surrounding as these might be or contain possible source habitats for the colonisation of paddy fields.
(2) Intensified management has a positive effect on weeds due to higher nutrient availability by increased fertiliser application but a negative effect on spider and planthopper communities because of the harmful effect of insecticides.
(3) Weed cover and richness affects spider as well as planthopper populations. A diverse herb structure benefits spiders by providing more opportunities for web construction or hiding places while high weed richness may create a less attractive location for planthoppers.
(4) The planthopper population is reduced by spider abundance and richness.

MATERIAL AND METHODS

Study Area

Wayanad District of Kerala State, South India is an undulating plateau abruptly descending in the west to Kerala plains but merging imperceptibly with the Mysore plateau in the east (Fig. S1). The elevation ranges from 700 to 2100 meters above MSL. The climate is tropical with an annual rainfall of 2,322 mm and a mean temperature range of 18 °C to 29 °C. The District covers an area of 212,560 ha of which approximately 97 % are under agricultural use, mostly subsistence farming and small holder plantations (Santhoshkumar & Ichikawa 2010). Located on the hill-tops are farm houses surrounded by homegarden polycultures containing fruit and timber trees, coffee, spices, coconut palms, arecanut, vegetables etc. that supply the households with food. Rice paddies are cultivated in the plains, predominantly during the Nancha season which starts with the southwest monsoon in July and ends with the harvest in December (Kumar et al. 2010). Starting in mid-1960s traditional paddy cultivation was transformed by the influences of the Green Revolution, one of the most considerable intervention in rice production in Asia, aimed at increasing rice production by fertiliser and pesticide application, the cultivation of high yielding varieties and the use of machinery, amongst others (Settle et al. 1996; Horgan & Crisol 2013). Such interventions have also reached, with some delay, such remote areas as Wayanad and are still ongoing. Furthermore, by the end of the 1990s the commercialisation of agriculture and the introduction of cash crops such as banana, arecanut, ginger and turmeric led to changes in land-use patterns in Wayanad. Cash crops are less labour demanding and by far more profitable than paddy cultivation (George & Krishnaprasad 2006, personal communication with farmers). This development resulted in a decline in paddy area in Wayanad from 30,000 ha in 1980-81 to 8,995 ha in 2011-12 (GOI 2013) and further in the transformation of increasing area of homegarden polycultures into plantations for rubber for instance. Despite all this, many farmers in Wayanad still continue paddy cultivation.

Experimental design

Paddy fields with high-intensity and low-intensity management adjacent to both diverse, structurally complex homegarden polycultures and banana monocultures were selected to cover agricultural intensification and land-use change at two spatial scales (Fig. 1). Three transects were established in each field: at the very edge of the paddy field adjacent to other habitats, 10 m into the field (centre) and at the earthen bund in the midst of the fields, to quantify the variation within the field and to account for possible edge effects. Along each transect, samples were taken within four subplots, each 2 x 1 meter in size (Fig. 2).

In total 18 paddy fields were selected and consent to work in their fields was given in written form by the famers. A first classification into high-intensity and low-intensity fields was based on interviews with the farmers about their cultivation practices. Since the farmers tended to be not strictly consistent in their cultivation practices, but often change it from year to year, actual management practices were noted during the sampling seasons in 2011 and 2012. For the analysis we focused on the relative importance of the major practices: amount of fertiliser application (kg/ acre) and frequency of insecticide application and weeding operations.

Figure 1: Paddy fields adjacent to homegarden polycultures (left) and banana monocultures (right).

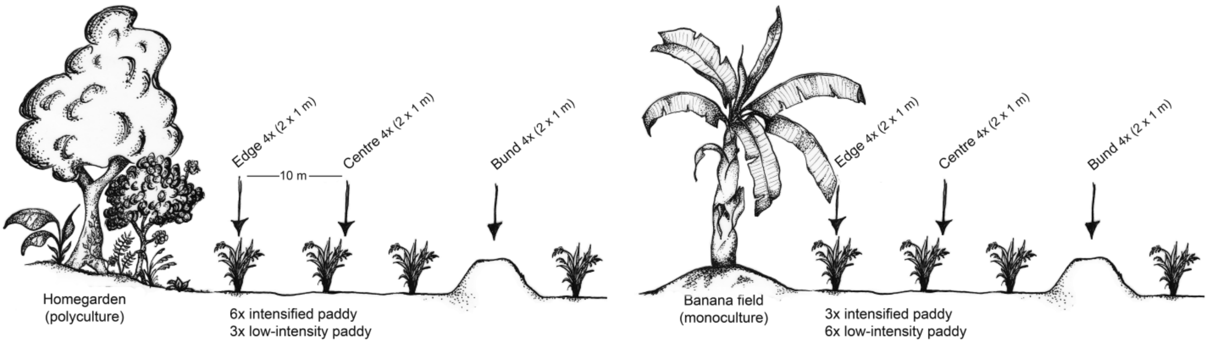


Figure 2: Experimental design. In total 18 paddy fields were sampled. Paddy fields with either high-intensity or low-intensity management were located adjacent to either homegarden polycultures or simplified banana monocultures. In each field three transects (edge, centre, bund) containing four subplots (2 x 1 m each) were selected.

Data collection

Data were collected after the southwest monsoon in 2011 and 2012, starting at the end of August about two weeks after the paddy was transplanted. Sampling was conducted between 8 am and 2 pm on days predominantly without rain. Arthropods were sampled during tillering, panicle initiation, flowering and milk ripening stage of the paddy (the latter only 2012). Specimens were caught by sweep netting; pitfall traps could not be installed due to standing water in the fields. Insects were transferred from the net into collection bottles filled with Isopropyl Alcohol while spiders were kept in separate bottles containing a small cotton ball soaked with Ethyl Acetate. All samples were taken to the lab for subsequent counting and identification. Spiders and planthoppers were identified to species level if possible, otherwise grouped into morphospecies. Spider identification followed Tikader (1987); Barrion & Litsinger (1995); Murphy & Murphy (2000); Proszynski (2003); Jocqué & Dippenaar-Schoeman (2007) and Sebastian & Peter (2009). Planthopper identification was done only for the 2012 collection and followed Kalshoven (1981). All other insects were counted and sorted into orders. Identification was done by LB. Dr. Sunil Jose double-checked and identified spider species in a few case of doubt. Arthropod specimens were preserved in 70 % Isopropyl Alcohol and were donated to the collection of the Zoological Survey of India, WGRC Calicut.

A plant survey was conducted in 2012 during panicle initiation and milk ripening. Plant species were identified in the field, only unknown species were collected for further identification in the lab. Individual numbers and percentage of coverage per species were recorded as well. Plants were identified by PP. Collected plant specimen were prepared and are stored at the Community Agrobiodiversity Centre, Puthoorvayal.

Taxonomy of spider and planthopper specimens follows World Spider Catalog (2014) and Encyclopedia of Life (EOL) respectively. Plants were double checked with Sasidharan (2011) and The Plant List (2013).

In order to estimate the complexity of the surrounding landscape, land-use types were mapped within a 500 m radius around each field based on Google Earth images. Current land-use was double-checked in the fields and maps were digitised in ArcGIS 10 (ESRI 2011). We calculated the compositional landscape heterogeneity as Shannon's diversity index of different habitat types and the number of patches of each habitat type.

Statistical analysis

To account for missing samples in few of the plots we calculated the mean value of all samples for each subplot. Data were than pooled per transect to get a stronger sample basis. We applied structural equation modelling (SEM) to evaluate the relations between land-use, management, weeds, planthoppers and spiders using the lavaan package (0.5-17) (Rosseel 2012) in the statistical software R (3.1.2) (R Core Team 2014). SEM is a statistical approach to analyse hypothesised interactions among several variables. Basically SEMs consists of multiple linear regressions and model-fitting analysis. The advantage of SEMs is that one variable can be an independent variable in one regression but an explanatory in another (Rosseel 2012). Dummy variables were created for the two categorical variables adjacent habitat (homegarden = 0, banana field = 1) and transect (edge = 1, centre = 2, bund = 3) and all variables were standardised. To account for non-normality of some variables we used the estimator "MLR" i.e. maximum likelihood with robust standard errors and a scaled test statistic. As we considered the experimental variables to be independent we did not allow for interactions between them. Goodness of fit was assessed by a χ^2 test ($P > 0.05$ indicates good fit) and comparative fit indices (CFI), which indicates the difference from the independent model (> 0.95 suggests significance). The Root Mean Square Error Aproximation (RMSEA) assesses the deviation between data and model (differences between the mean covariance residuals); a value of zero indicates no deviation.

RESULTS

In total 2073 spider individuals of 86 species from 15 families and 15411 planthopper individuals were collected. A total of 38350 plant individuals of 29 families and 95 species were recorded. The most abundant spider family was Tetragnathidae (n = 1024, dominated by *Tetragnatha maxillosa*), followed by Oxyopidae (n = 458, *Oxyopes javanus*) and Salticidae (n = 255, mainly *Carrhotus viduus*) (Table S1). Most frequent plant families were Cyperaceae (n = 8205), Lythraceae (n=7536) and Poaceae (n = 5590) (Table S2). Planthopper population was dominated by agrobiont species, namely *Sogatella furcifera* (Delphacidae), *Nephotettix* spp. (Cicadellidae) and *Recilia dorsalis* (Cicadellidae) (Table S3); all are known to be potential pest species in paddy cultivation systems (Kalshoven 1981; Settle et al. 1996).

The results of the structural equation model (Fig. 3 & Table S4) showed that adjacent banana fields benefited planthopper abundance (Fig. 4) and weed richness in the paddy fields (standardised path coefficients $\beta = 0.28$ and 0.22 respectively). Furthermore, planthopper abundance was promoted by a higher density of grasses (Poaceae) ($\beta = 0.33$) (Fig. 5), but negatively affected by increasingly diverse weed community. In contrast, spider species richness was enhanced by increasing weed diversity. However, more important than weed richness was the effect of planthopper abundance and fertiliser application on spiders. The more planthoppers occur in the field the higher the number of spider individuals ($\beta = 0.22$) (Fig. 6) and species ($\beta = 0.13$). We considered the amount of applied fertiliser (kg/ acre), frequency of insecticide application and weeding operations separately to quantify their relative importance in shaping the community structure. Only the amount of fertiliser remained in the minimal adequate model, explaining variation in the spider community. Increased application of fertiliser resulted in a slight increase in spider abundance and richness. Furthermore, weed richness (β = 0.11) and grass density (β = 0.14) increased slightly, however, this effects were not significant. The within field location (edge, centre, bund) strongly affected all observed taxonomic groups. Spider abundance and richness, grass density and the number of planthoppers declined from the edge of the paddy field (close to adjacent habitat) towards the bund in the midst of the field. Weed richness showed a contrasting pattern, as it was highest at the bund. A closer look at this within field variation revealed that spider abundance continuously declined from edge to centre and finally to the bund (less pronounced for spider richness), whereas planthopper abundance, grass density and weed richness showed no significant differences between edge and centre (Fig. 7).

The landscape complexity within a 500 m radius around the fields appeared to have no significant effects. Additionally, we tested individual landscape elements e.g. homegardens, fallows, etc. but no effect was found.

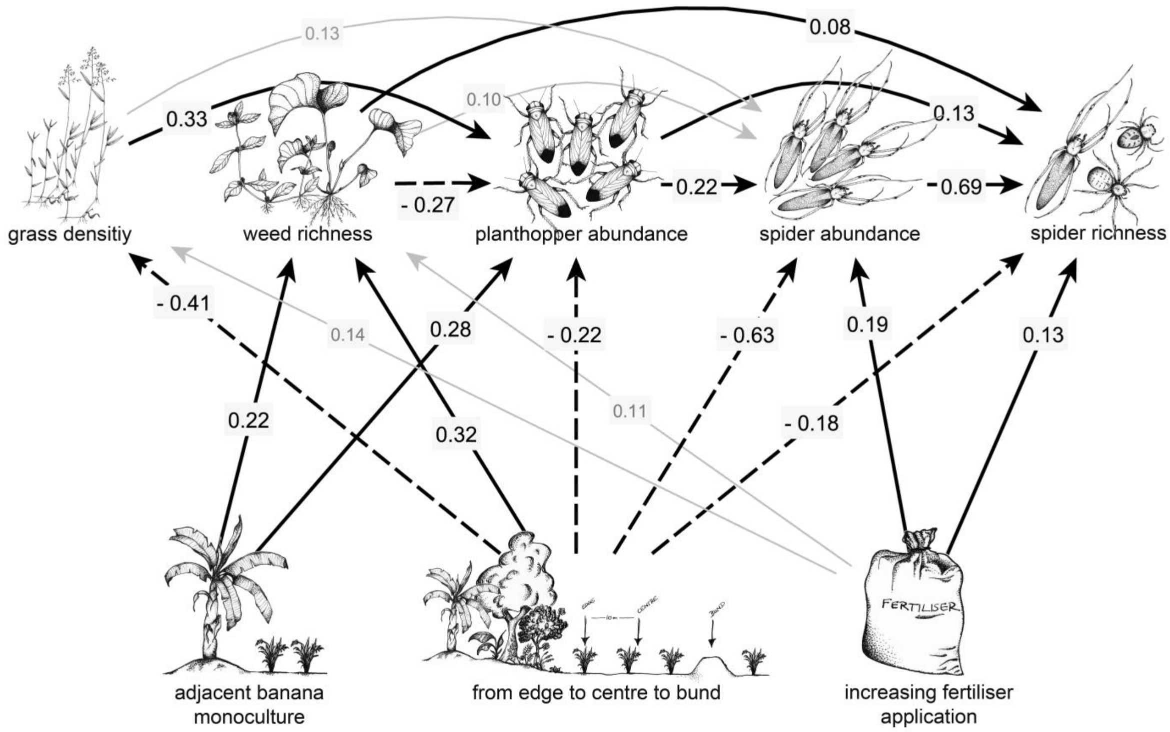


Figure 3: The graph shows the results of the structural equation model with N = 54, χ^2 = 3.484, P = 0.942, 9 degrees of freedoms, Comparative Fit Index = 1.000, Root Mean Square Error of Approximation = 0.000 and Standardized Root Mean Square Residual = 0.029. Solid arrows show positive, dashed arrows negative effects, grey arrows indicate non-significant effects. Numbers attached to the arrows are standardised path coefficients. Categorical variables were specified as numeric variables: adjacent habitat: homegarden = 0, banana field = 1; within field location: edge = 1, centre = 2, bund = 3.

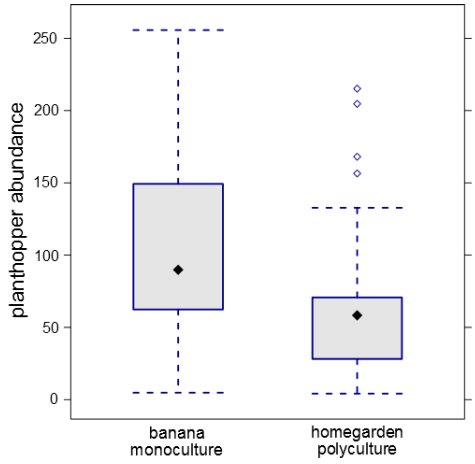


Figure 4: Differences in planthopper abundance beside homegarden polycultures and banana monocultures.

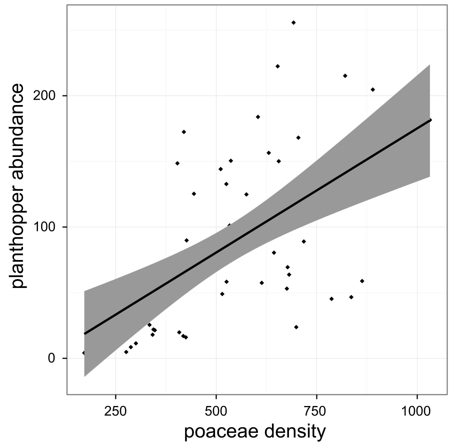


Figure 5: Planthopper abundance in relation to Poaceae density (shoots per 2 x 1 m) in the paddy fields. Pearson correlation coefficient = 0.55, P <0.001.

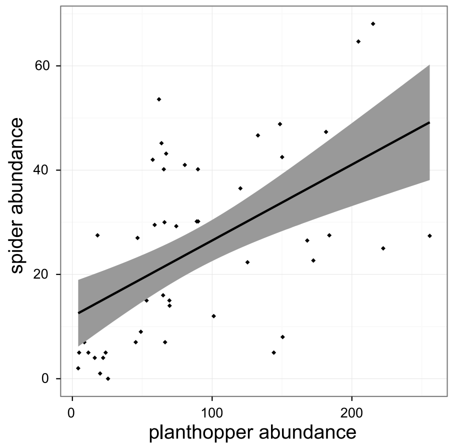


Figure 6: Spider abundance in relation to planthopper abundance in the paddy fields. Pearson correlation coefficient = 0.55, P <0.001.

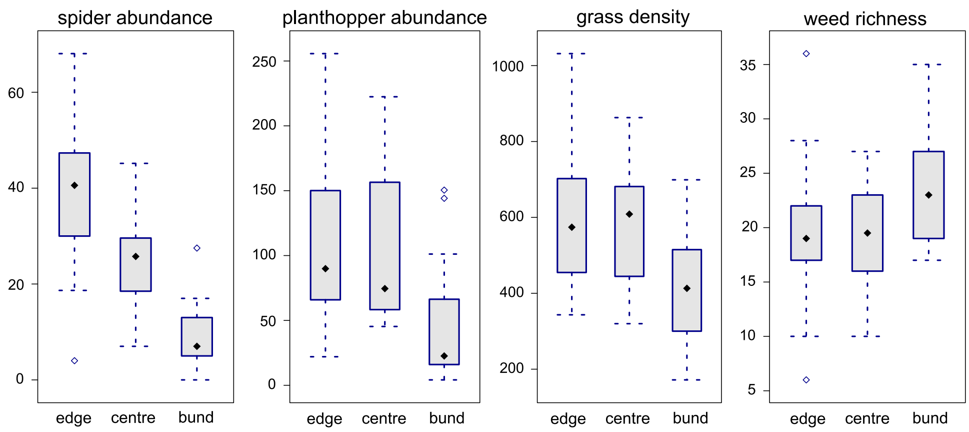


Figure 7: Spider and planthopper abundance, grass density and weed richness at the edge, centre and bund of paddy fields.

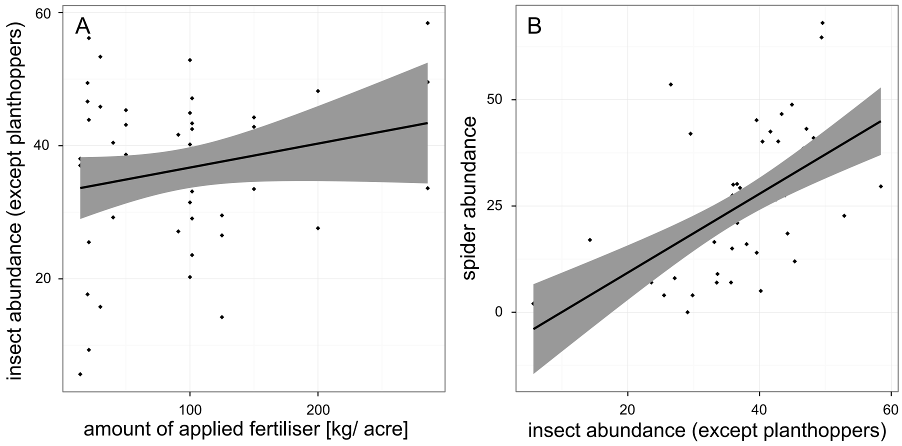


Figure 8: (A) Correlation between insect abundance and increased fertiliser application (Pearson correlation coefficient = 0.22, P = 0.11) and (B) correlation between spider abundance and insects (0.62, P < 0.001).

DISCUSSION

Our results showed that banana monocultures enhanced weed richness and planthopper abundance in adjacent paddy fields. The number of planthoppers was positively related to the density of weedy grasses (Poaceae), whereas the diversity of weeds (dominated by dicots) negatively affected planthoppers. Spiders on the other hand benefitted from weed diversity as well as from increased planthopper (prey) density. Fertiliser application had a positive effect on spider population and on weed richness and grass density. From paddy field edges to the centre and finally, to the bund spider abundance an richness decreased, indicating influences of adjacent habitats on paddy field colonisation.

Adjacent habitat

Banana monocultures adjacent to paddy fields promoted the abundance of planthoppers as well as species richness of weeds in the paddy fields. Banana monocultures in Wayanad are transformed paddy fields. As banana plants, unlike paddy, requires dry soil the fields are drained by building rows of small, parallel dams on which the banana plants are planted. The water drains off through the channels between the dams. Due to this transformation the weed community in banana fields may still be similar to that in the paddy fields and hence could be a source for the colonisation of paddy fields. Furthermore, banana fields are established for one or two years in contrast to about five months in case of paddy and we observed that weed growth was usually controlled only in the early stage of the banana growth but was neglected in older banana fields. Moreover, fertilisers applied to banana monocultures may reach the paddies through the channels. This additional nutrient supply may have benefitted weed growth also and probably enhanced the nutritional value of weed and paddy, thereby increasing their attractiveness for planthoppers (Lu & Heong 2009; Horgan & Crisol 2013).

Grass density and weed richness

Higher grass density had an even stronger effect on planthopper abundance than adjacent banana fields. Although pest species like *Sogatella furcifera* or *Nephottetix* spp. are specialised on paddy plants on which they suck on leaves or stalks, poaceous weeds are alternative host plants and an additional food source (Kalshoven 1981; Khan et al. 1991). Poaceae are amongst the first weeds to migrate into the paddy fields after their preparation and thus possibly facilitate population build-up of planthoppers in the early stage of the paddies (Bambaradeniya et al. 2004). Takada et al. (2012) found such a positive relation to alternative hosts of the rice grain sucking mirid bug.

Weed diversity on the other hand had a negative effect on planthoppers. Increasing diversity in weed species is mainly driven by an increase in dicotyledonous plants, which do not serve as host plants for the planthopper pest species. High diversity of non-host plants can reduce the number of planthoppers, because those habitats are less attractive (Heong et al. 2014). Furthermore, increasing diversity of herbaceous weeds slightly enhanced spider species richness, probably due to increased structural diversity which provides web building spiders more options to fix their webs or offers shelter for free hunting spiders (Marc et al. 1999; Sunderland & Samu 2000; Tahir & Butt 2009). However, the weed diversity effect found in this study was comparatively low, suggesting that other factors such as the prey availability were more important for spider population.

Planthopper abundance

Planthopper abundance may be controlled by the spider population in paddy fields as argued by Maloney et al. (2003). In this study, however, spider population was driven by the availability of planthoppers which indicates a bottom up effect (Marc et al. 1999). Although spiders do show certain prey preferences, they are able to switch these preferences in response to whichever type of prey is most abundant (Nyffeler et al. 1994; Riechert & Lawrence 1997). The most abundant spider was *Tetragnatha* spp. (Tetragnathidae) one of the most frequently found spider family in paddy fields (Sebastian et al. 2005; Takada et al. 2012). *Tetragnatha* species build fairly large horizontal webs in the paddy canopy and are known to prefer wetland habitats and also paddy fields. According to Kiritani et al. (1972) Tetragnathidae contributed significantly to planthopper reduction. The second most abundant spider, the free hunting *Oxyopes javanus*, is known to prey on planthoppers as well. The consumption of *S. furcifera* (Delphacidae) by *Oxyopes* *javanus* (Oxyopidae) increased with increasing abundance of this planthopper (Butt & Xaaceph 2015).

Fertiliser application

The positive effect of fertiliser application on spiders might be explained by an indirect effect of increased productivity and a related rise in the density of potential prey for spiders. Although planthopper abundance did not respond to higher amounts of fertiliser, the number of other insects increased. Spider abundance in turn was positively related to insect abundance (Fig. 8 A & B). Our analysis also showed a positive, yet not significant response, of weed richness and grass density to increased fertiliser application as reported by Major et al. (2005). This could be another indirect effect of fertilisers on spiders, through weed richness and through a positive effect of grass density on planthopper abundance.

Within field location: from edge to centre to bund

As a rice field is frequently disturbed by agricultural management and cleared totally after harvest and ploughing, spiders, planthoppers and weeds need to immigrate from the surroundings (Bambaradeniya et al. 2004; Bianchi et al. 2006; Rand et al. 2006).

Planthopper abundance and grass density did not differ between edge and centre but were lower at the bund. Planthoppers, highly mobile, apparently spread out easily but prefer to stay with their preferred host plant in the paddy patches. Two of the most abundant grass species, namely *Isachne globosa* and *Eragrostis unioloides*, wetland species and well known weeds in paddy fields (Bambaradeniya et al. 2004), were found much more frequently in the paddy patches compared to the bunds. Perhaps the pattern found for grass density is driven by these two species

Despite great variation in the management of the bunds, some were kept completely barren while others were totally overgrown, overall weed richness was higher at the bunds compared to the paddy patch. As paddy does not grow at the bunds, plants find themselves without competition there and hence can spread freely if not removed by the farmers. Furthermore, the standing water in the paddy patches during most of the season may hinder some plant species of growing there.

Despite the evenly distributed planthoppers, spiders seem to expand less easily. Their abundance and richness steadily decreased from edge to centre to bund. Compared to planthoppers spiders are less mobile and usually do not walk long distances through the field if not necessary. If prey is sufficiently available where ever they land first after entering the paddy fields they simply may remain there (Marc et al. 1999; Harwood et al. 2001). This suggests that spider colonisation of paddy fields was affected by adjacent habitats as shown by Tahir & Butt (2009) and described from other crops e.g. winter wheat by Clough et al. (2005). The type of the adjacent habitat, banana monoculture vs homegarden polyculture, did not exhibit direct effects on spiders, yet an indirect effect of banana fields via planthopper density is possible.

CONCLUSION

The results of this study showed that banana monocultures adjacent to paddy fields benefit weed richness and planthopper abundance. Furthermore, planthoppers were promoted by a higher density of weedy grasses in the fields but negatively affected by weed richness. Spiders in contrast benefited from weed richness, yet the major determining factor seemed to be the availability of prey. Increased application of fertiliser appeared to have an indirect effect on spider population by promoting the numbers of insects and therefore prey. Furthermore, weed richness and grass density slightly increased with higher amounts of fertiliser which could be another indirect fertiliser effect on spiders. Spider abundance and richness declined from field edge to centre to bund indicating an influence of adjacent habitat on paddy field colonisation. Considering the effects of fertiliser application, grass density, planthopper abundance and spider richness and abundance the results suggest that the paddy agroecosystems in Wayanad are mainly driven by bottom up effects as it appears that resources control the consumer abundance.

Overall, the results suggest that paddy cultivation in Wayanad needs to consider the identity of habitats adjacent to paddy fields and weed identity (dicots vs monocots). Furthermore, fertilisers should be applied with care - if necessary at all - to maintain a balanced paddy agroecosystem.

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APPENDIX

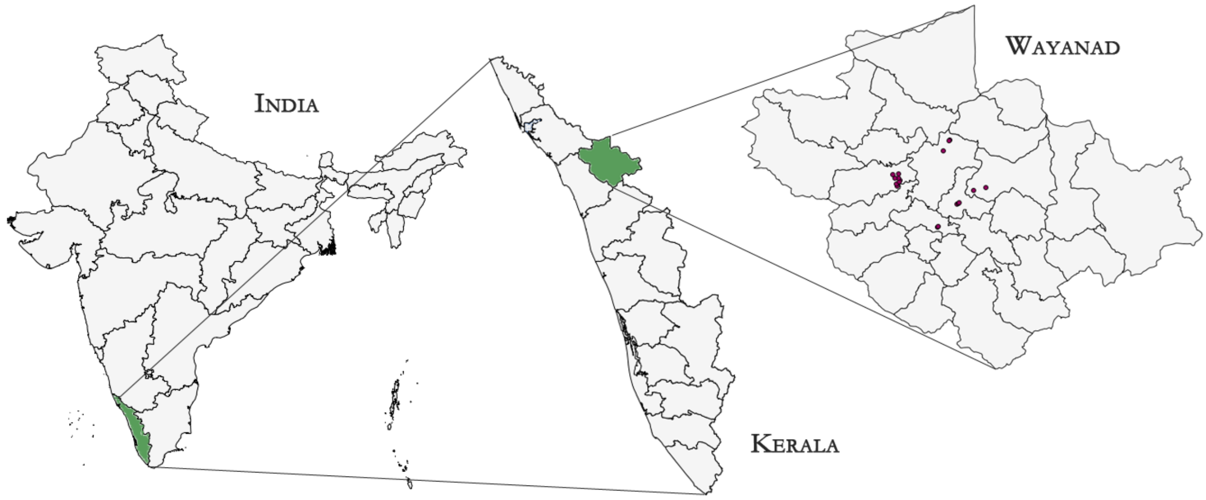


Figure S1: Map of the study region Wayanad in Kerala, India.

Table S1: Spider specimen collected in 18 paddy fields in Wayanad, South India in 2011 and 2012.

Species	# individuals	Guild
Sp. 1	2	
n.i.	27	
Araneidae	**111**	orb weaver
Araneus ellipticus (Tikader & Bal, 1981)	15	
Araneus n.i.	5	
Araneus sp. 14	2	
Argiope aemula	1	
Argiope catenulata (Walckenaer, 1841)	1	
Argiope sp.	1	
Argiope sp. 2	1	
Argiope sp. 8	1	
Cyrtarachne sp. 13	1	
Cyrtophora cicatrosa (Stoliczka, 1869)	1	
Cyrtophora sp. 19	1	
Cyrtophora sp. 21	1	
Cyrtophora sp. 4	1	
Eriovixia laglaizei (Simon, 1877)	2	
Gea sp.	1	
Larinia phthisica (L. Koch, 1871)	8	
Neoscona sp.	48	
Neoscona sp. 6	2	
Ordgarius sp.	3	
n.i.	15	
Clubionidae	**12**	foliage runner
Clubiona sp.	11	

n.i.	1	
Corinnidae	**2**	ground runner
Castianeira zetes Simon, 1897	1	
Corinnomma sp. 1	1	
Linyphiidae	**60**	space web builder
Atypena adelinae Barrion & Litsinger, 1995	37	
sp. 4	2	
n.i.	21	
Lycosidae	**61**	ground runner
Pardosa heterophthalma (Simon, 1898)	1	
Pardosa pseudoannulata (Bösenberg & Strand, 1906)	2	
Pardosa sumatrana (Thorell, 1890)	31	
Pardosa sp. 1	2	
Pardosa sp.	19	
n.i.	6	
Oxyopidae	**458**	stalker
Oxyopes birmanicus Thorell, 1887	1	
Oxyopes javanus Thorell, 1887	164	
Oxyopes sp.	293	
Philodromidae	**2**	ambusher
Philodromus	1	
n.i.	1	
Pholcidae	**1**	space web builder
Pisauridae	**4**	ambusher
Nilus albocinctus (Doleschall, 1859)	2	
Perenethis venusta L. Koch, 1878	1	
Pisaura	1	
Salticidae	**255**	stalker
Bianor	6	
Bianor sp. 1	1	
Bianor sp. 11	3	
Bianor sp. 14	5	
Bianor sp. 2	20	
Bianor sp. 20	1	
Bianor sp. 28	1	
Bianor sp. 3	2	
Bianor sp. 5	3	
Bianor sp. 6	12	
Bianor sp. 7	6	
Carrhotus sp. 12	1	
Carrhotus sp. 16	1	
Carrhotus sp. 21	2	
Carrhotus viduus (C. L. Koch, 1846)	139	
Chalcotropis pennata Simon, 1902	1	
Epeus indicus Prószyński, 1992	3	
Harmochius brachiatus (Thorell, 1877)	13	
Hylleae sp. 24	1	

Myrmarachne orientales Tikader, 1973	1	
Phintella sp. 15	5	
Plexippus sp. 25	1	
sp. 23	1	
sp. 26	3	
sp. 27	1	
sp. 29	1	
sp. 30	1	
sp. 31	1	
sp. 33	1	
n.i.	18	
Tetragnathidae	**1024**	orb weavers
Leucauge decorata (Blackwall, 1864)	1	
Leucauge	3	
Tetragnatha ceylonica O. Pickard-Cambridge, 1869	59	
Tetragnatha javana (Thorell, 1890)	55	
Tetragnatha mandibulata Walckenaer, 1841	4	
Tetragnatha maxillosa Thorell, 1895	236	
Tetragnatha sp.	575	
Tetragnatha sp. 14	1	
Tetragnatha sp. 5	1	
Tetragnatha virescens Okuma, 1979	3	
Tylorida	6	
Tylorida striata (Thorell, 1877)	47	
Tylorida ventralis (Thorell, 1877)	4	
Tylorida xavieri Jose, 2005	2	
Tylorida culta (O. Pickard-Cambridge, 1869)	1	
sp. 15	1	
n.i.	25	
Theridiidae	**11**	space web builder
Achaearanea	1	
Argyrodes sp. 1	1	
Chrysso	1	
Enoplognatha	4	
Phycosoma martinae (Roberts, 1983)	1	
Theridion	1	
Theridula angula (Tikader, 1970)	1	
n.i.	1	
Theridiosomatidae	**1**	orb weaver
Wendilgarda sp.	1	
Thomisidae	41	ambusher
Carmaricus formosus Thorell, 1887	1	
Henriksenia hilaris (Thorell, 1877)	9	
Misumena	3	
Misumena sp. 15	2	
Oxytate sp. 3	1	
Oxytate *virens* (Thorell, 1891)	2	

Thomisus lobosus Tikader, 1965	1	
Thomisus	3	
Thomisus pugilis Stoliczka, 1869	6	
Thomisus sp. 1	3	
Thomisus sp. 2	1	
Tmarus sp. 10	2	
Xysticus sp. 18	1	
Xysticus sp. 9	1	
sp. 12	1	
n.i.	4	
Uloboridae	**1**	orb weaver
Zosis geniculata (Olivier, 1789)	1	

Table S2: Plant species identified from 18 paddy fields in Wayanad, South India in 2012.

Species	# Individuals	mean % cover	Usage
Amaranthaceae	**450**		
*Alternanthera pungens*Kunth	330	0.414	Food
Alternanthera sessilis(L.) R. Br. ex DC.	115	0.137	Food
*Amaranthus viridis*L.	5	0.005	Food
Apiaceae	**805**		
Centella asiatica(L.) Urb.	805	0.944	Medicine
Araceae	**9**		
Cryptocoryne retrospiralis(Roxb.) Kunth	9	0.019	Food
Asteraceae	**1523**		
Acmella calva(DC.) R.K. Jansen	8	0.013	Medicine
Acmella uliginosa (Sw.) Cass.	63	0.046	Medicine
Ageratum conyzoides (L.) L.	323	0.285	Medicine/ Fodder
Blumea axillaris(Lam.) DC.	29	0.054	Medicine/ Fodder
Crassocephalum crepidioides(Benth.) S. Moore.	2	0.005	
Eclipta prostrata (L.) L.	165	0.151	
Emilia sonchifolia (L.) DC. ex DC.	16	0.013	Medicine/ Fodder
Grangea maderaspatana(L.) Poir.	631	0.871	
*Mikania micrantha*Kunth	6	0.013	Invasive
*Sphaeranthus indicus*L.	266	0.285	Medicine
Sphagneticola trilobata (L.) Pruski	2	0.003	Invasive
Spilanthes ciliata HBK	12	0.011	Medicine
Boraginaceae	**9**		
Hilotropium keralense Sivarajan & Manilal.	9	0.022	
Caryophyllaceae	**118**		
Drymaria cordata subsp. diandra (Blume) J.A.Duke	3	0.005	Food
Polycarpon prostratum(Forssk.) Asch. & Sehweinf.	115	0.263	
Commelinaceae	**222**		
*Commelina diffusa*Burm. f.	95	0.108	Food/ Medicine
Floscopa scandens Lour.	40	0.032	
Murdannia dimorpha (Dalzell) G.Brückn.	87	0.137	
Cyperaceae	**8205**		

*Cyperus difformis*L.	906	0.616	
Cyperus distans L. f.	255	0.134	
*Cyperus haspan*L.	469	0.258	Fodder
Cyperus iria L.	975	0.543	
*Cyperus javanicus*Houtt.	135	0.094	
*Cyperus tenuispica*Steud.	82	0.110	Fodder
Eleocharis dulcis (Burm.f.) Trin. ex Hensch.	175	0.231	
*Fimbristylis acuminata*Vahl	3	0.005	
Fimbristylis aestivalis Vahl	792	0.758	
Fimbristylis dichotoma (L.) Vahl	101	0.059	
Fimbristylis ferruginea(L.) Vahl	69	0.073	
Fimbristylis quinquangularis(Vahl) Kunth	697	0.605	
Fuirena ciliaris (L.) Roxb.	105	0.108	
Kyllinga nemoralis (J.R.Forst. & G.Forst.) Dandy ex Hutch. & Dalziel	271	0.288	
Lipocarpha chinensis (Osbeck) J.Kern	102	0.081	
Pycreus stramineus C.B.Clarke	120	0.067	
Schoenoplectiella juncoides (Roxb.) Lye	2948	0.812	Fodder
Eriocaulaceae	**1465**		
*Eriocaulon heterolepis*Steud.	138	0.124	
Eriocaulon quinquangulare L.	232	0.153	
Eriocaulon truncatum Buch.-Ham. ex Mart.	1095	0.946	
Euphorbiaceae	**9**		
*Euphorbia hirta*L.	9	0.016	Medicine/ Fodder
Fabaceae	**87**		
*Geissaspis tenella*Benth.	33	0.035	
Mimosa pudica L.	39	0.056	Medicine
Senna tora (L.) Roxb.	1	0.003	Food/ Medicine
*Smithia conferta*Sm.	14	0.008	Fodder
Gentianaceae	**508**		
Canscora diffusa (Vahl) R.Br. ex Roem. & Schult.	508	0.234	
Hydrocharitaceae	**770**		
Vallisneria natans (Lour.) H.Hara	770	1.766	
Hypericaceae	**56**		
Hypericum japonicum Thunb.	56	0.075	
Lamiaceae	**86**		
Leucas aspera(Willd.) Link.	6	0.011	Food/ Medicine
Pogostemon deccanensis(Panigrahi) Press	80	0.016	
Linderniaceae	**4370**		
Lindernia anagallis(Burm. f.) Pennell	2907	0.933	
Lindernia antipoda(L.) Alston	951	0.366	
Lindernia hyssopiodes (L.) Haines	358	0.148	
Lindernia caespitosa(Blume) Panigrahi	104	0.075	
Lindernia rotundifolia (L.) Alston	33	0.013	
Lindernia viscosa(Hornem.) Merr.	17	0.024	
Lythraceae	**7536**		
*Rotala malabarica*Pradeep, Joseph & Sivar.	1811	1.113	
Rotala malampuzhensis R.V.Nair ex C.D.K.Cook	94	0.134	

Rotala rotundifolia (Buch.-Ham. ex Roxb.) Koehne	5631	6.605	
Malvaceae	**132**		
*Sida acuta*Burm. f.	11	0.008	
*Waltheria indica*L.	121	0.000	Food/ Medicine
Marsileacea	**455**		
Marsilea minuta L.	455	0.640	Food/ Medicine
Molluginaceae	**16**		
Mollugo pentaphylla L.	16	0.013	
Onagraceae	**3313**		
Ludwigia hyssopifolia(G. Don) Exell	2313	2.438	
Ludwigia octovalvis (Jacq.) P.H.Raven	669	0.497	
*Ludwigia perennis*L.	10	0.008	
Ludwigia peruviana(L.) H. Hara	321	0.196	
Phyllanthaceae	**23**		
Phyllanthus amarus Schum. & Thonn.	15	0.035	Medicine
Phyllanthus urinaria L.	8	0.008	Medicine
Plantaginaceae	**153**		
Limnophila chinensis(Osbeck) Merr.	17	0.027	
Limnophila heterophylla (Roxb.) Benth.	7	0.013	
Mecardonia procumbens (Mill.) Small	2	0.005	
Scoparia dulsis L.	127	0.081	Food/ Medicine
Poaceae	**5590**		
Arundinella purpurea Hochst. ex Steud.	70	0.134	
Axonopus compressus(Sw.) P. Beauv.	364	0.468	
Digitaria ciliaris (Retz.) Koeler	29	0.040	
Echinochloa crus-galli(L.) P. Beauv.	56	0.097	Fodder
Eragrostis unioloides(Retz.) Nees ex Steud.	444	0.586	
Isachne globosa (Thunb.) Kuntze	2396	3.132	Fodder
Ottochloa nodosa (Kunth) Dandy	371	0.306	
*Panicum repens*L.	1608	1.301	Fodder
*Paspalum distichum*L.	109	0.360	
*Paspalum scrobiculatum*L.	43	0.067	Fodder
Sacciolepis indica(L.) Chase	62	0.070	Fodder
Sacciolepis interrupta (Willd.) Stapf	34	0.016	
Sacciolepis myosuroides(R. Br.) A. Camus	4	0.000	
Polygonaceae	**18**		
Persicaria chinensis (L.) H. Gross	18	0.019	Poison for fishing
Pontederiaceae	**1908**		
Monochoria vaginalis (Burm. f.) C. Presl	1908	1.884	Food
Pteridaceae	**2**		
Ceratoperis thalictroides (L.) Brongn.	2	0.005	
Rubiaceae	**211**		
*Oldenlandia corymbosa*L.	211	0.231	
Salviniaceae	**301**		
Azolla pinnata R. Br.	250	0.387	N Fertiliser
Salvinia adnata Desv.	51	0.027	

Table S3: Leaf- and planthopper species collected in 18 paddy fields in Wayanad, South India in 2011 and 2012. Species were not identified for the 2011 sample.

Planthoppers 2011	**# Individuals**
Auchenorrhyncha	5253

Planthoppers 2012

Species	**# Individuals**
Aphrophoridae	**3**
Cercopidae	**13**
Cicadellidae	**5484**
Nephotettix	2
Nephotettix nigropictus (Stål, 1870)	1109
Nephotettix virescens (Distant 1908)	788
Recilia dorsalis Motschulsky 1859	573
chocolate brown	2
green	27
light green	548
transparant	827
white	4
yellow head	1417
n.i.	187
Cixiidae	**1**
Delphacidae	**2408**
Nilaparvata lugens (Stål, 1854)	266
Sogatella furcifera (Horváth, 1899)	2103
n.i.	39
Dictyopharidae	**9**
Fulgoromorpha	**1**
Issidae	**340**
Tettigometridae	**1**
nymphe	**2107**

Table S4: Results from the structural equation model (Fig. 3).

Sample size:

Number of observations	54
Number of missing patterns	1

Indices of model fit:

Estimator	ML	Robust
Minimum Function Test Statistic	3.699	3.484
Degrees of freedom	9	9
P-value (Chi-square)	0.930	0.942
Scaling correction factor for the Yuan-Bentler correction		1.062

Parameter estimates:

Information	Observed
Standard Errors	Robust.huber.white

	Estimate	Std.err	Z-value	P(>|z|)	Std.lv	Std.all
Regressions:						
plants~						
ferti	0.044	0.051	0.858	0.391	0.044	0.112
HAB	0.19	0.108	1.764	0.078	0.19	0.217
TRANS	0.236	0.094	2.502	0.012	0.236	0.324
poaceae~						
TRANS	-0.345	0.108	-3.211	0.001	-0.345	-0.407
ferti	0.062	0.049	1.265	0.206	0.062	0.136
cic.abu~						
HAB	0.6	0.23	2.609	0.009	0.6	0.275
TRANS	-0.397	0.184	-2.156	0.031	-0.397	-0.219
plants	-0.663	0.242	-2.746	0.006	-0.663	-0.266
poaceae	0.866	0.252	3.44	0.001	0.866	0.405
spi.abu~						
ferti	0.17	0.067	2.538	0.011	0.17	0.185
TRANS	-1.068	0.171	-6.232	0	-1.068	-0.627
poaceae	0.26	0.185	1.403	0.161	0.26	0.129
cic.abu	0.207	0.12	1.721	0.085	0.207	0.22
plants	0.226	0.21	1.076	0.282	0.226	0.097
spi~						
ferti	0.108	0.036	2.984	0.003	0.108	0.132
TRANS	-0.271	0.112	-2.431	0.015	-0.271	-0.178
spi.abu	0.617	0.077	8.063	0	0.617	0.688
cic.abu	0.11	0.047	2.317	0.021	0.11	0.13

	plants	0.171	0.096	1.778	0.075	0.171	0.082
Intercepts:							
	plants	46.515	10.692	4.35	0	46.515	1.861
	poaceae	108.935	12.278	8.872	0	108.935	3.745
	cic.abu	52.337	34.155	1.532	0.125	52.337	0.841
	spi.abu	101.442	33.983	2.985	0.003	101.442	1.737
	spi	22.531	13.986	1.611	0.107	22.531	0.43
	ferti	86.698	8.682	9.986	0	86.698	1.359
	HAB	85.5	3.878	22.045	0	85.5	3
	TRANS	84	4.667	18	0	84	2.449
Variances:							
	ferti	4070.554	987.014	4070.554	1		
	HAB	812.25	0	812.25	1		
	TRANS	1176	113.161	1176	1		
	plants	522.239	112.053	522.239	0.836		
	poaceae	690.143	114.882	690.143	0.816		
	cic.abu	2083.226	371.408	2083.226	0.538		
	spi.abu	1075.845	204.527	1075.845	0.315		
	spi	386.876	81.288	386.876	0.141		
R-Square:							
	plants	0.164					
	poaceae	0.184					
	cic.abu	0.462					
	spi.abu	0.685					
	spi	0.859					

plants = weed richenss, ferti = fertiliser application, HAB = adjacent habitat (homegarden polyculture/ banana monoculture), TRANS = transect (edge/ centre/ bund), poaceae = grass denistiy, cic.abu = planthopper abundance, spi.abu = spider abundance, spi = spider richness.

Chapter 2

SPIDER FAMILIES AND SPIDER WEBS IN INDIAN RICE FIELDS – AN ASSESSMENT OF LOCAL AND LANDSCAPE EFFECTS

ABSTRACT

Spiders are omnipresent and occur in almost all terrestrial habitats, also in agricultural fields. Applying several foraging strategies and utilising different microhabitat and prey species, spiders can be effective control agents of insect pests. However, agricultural intensification can have negative effects on these predators. In this study we examine how different spider families from South Indian rice fields respond to prey abundance and agricultural intensification at different special scales. Additionally, we investigate whether spider web surveys can provide valuable additional information. For this, rice fields with low-intensity or high-intensity management located either next to homegarden polycultures or banana monocultures were selected. Furthermore, the landscape structure in the surrounding of the fields was recorded and a plant survey was conducted to assess weed richness and cover. The results showed that the major determining factor for overall spider and web abundance was the availability of potential insect prey; hence the spider community in these paddy fields was driven by bottom up effects. A closer look at different families and web types revealed differences within this general pattern. The web building Tetragnathidae and Linyphiidae responded mainly to Lepidoptera and leafhopper abundance while Araneidae were linked to Lepidoptera. The hunting spider Oxyopidae responded positively to all insects groups. For this family we also found a slight negative effect of increasing herb cover in the paddy fields. The two other hunting spider families, Salticidae and Lycosidae, were only correlated with increasing numbers of Lepidoptera. No effect was found for adjacent habitat (monoculture vs polyculture) and the structure of the surrounding landscape. However, higher percentage of fallows showed a positive effect on ground webs. Furthermore, fertiliser and insecticide application did not show any effect, suggesting that the level of intensification not yet reached a critical point. The results further showed that spider web sampling can be a useful addition to spider sampling, as, for example, the diverging results for orb webs vs Araneidae and ground webs (Erigoninae, Linyphiidae) and Linyphiidae suggested. In conclusion, our results showed that in the Indian study region with in general relatively low intensity of agriculture, a bottom-up effect appeared to be the major determinant of generalist predators such as spiders.

Key words: Araneae, agricultural intensification, spider webs, paddy, land-use change

INTRODUCTION

Spiders (Araneae) are omnipresent, generalist predators and they occur in almost all terrestrial habitats (Murphy & Murphy, 2000; Foelix, 2011). As carnivores they mainly prey on insects and arthropods especially spiders, with some exceptions like fishing for tadpoles (Schulze & Janssen, 2010), feeding on bats and birds (Nyffeler & Knörnschild, 2013), drinking nectar (Pollard, 1993), or even becoming vegetarian (Meehan et al., 2009). Spiders can be grouped into web builders and free hunters, while these two foraging strategies can be further subdivided. Uetz et al., 1999 for instance differentiated between eight guilds in agricultural fields: sheet, tangle, orb and space web-building spiders and running, stalking, ambushing and foliage-dwelling, free-hunting species.

Spiders also occur in agricultural fields, often in high abundance and richness (e.g. Marc et al., 1999; Sunderland & Samu, 2000; Sebastian et al., 2005; Stenchly et al, 2012; Takada et al., 2012). The broad food spectrum of spiders leads to quite stable population dynamics and allows them to remain in agricultural fields in times of low abundances of preferred prey species (Maloney et al., 2003). Because spiders are generalist predators but utilise diverse foraging strategies and exhibit specialisations with respect to microhabitat, prey items or active periods, they can be very useful natural enemies for insect pests (Marc et al., 1999; Maloney et al., 2003). Spiders are also highly abundant in rice fields and several studies describe their role as important biocontrol agents to reducing populations of several rice pests such as leaf- and planthoppers or mirid bugs (e.g. Nyffeler & Benz, 1987, Kiritani et al., 1972, Sebastian et al., 2005, Takada et al., 2012, Takada et al., 2013, Lou et al., 2013).

Rice is the major food crop in Asia. To meet the demands of the growing population, the Green Revolution in the 1960 aimed to increase the rice production through the introduction of agrochemicals, machinery and high yielding varieties. However, intensified cultivation practices may affect the prey-predator complexes in agricultural fields (Zhao et al., 2015a, Lee et al., 2014). Fertiliser application can promote the pests' populations. Especially sap-feeding insects like leafhoppers, one of the major pests of rice crop, respond positively to nitrogen-rich plants (Matson, 1997; Lu & Heong, 2009; Horgan & Crisol, 2013). Pesticide application kills the target species but often also useful natural enemies (Settle et al., 1996; Marc et al., 1999; Landis et al., 2000; Tilman et al., 2001). For instance, pesticides applied against pests in the early growth of paddies also kills predators like spiders, which are then missing to control pests that peak later in the season, such as plant- and leafhoppers, which are a major concern in rice cultivation (Settle et al., 1996; Lou et al., 2013; Lu et al., 2014). Furthermore, weed density provides higher structural diversity in a habitat which benefits spider communities positively (Balfour & Rypstra, 1998; Sunderland & Samu, 2000). Weeding may reduce this structural diversity in the crop field and thus can also lead to a decline in spider abundance and richness.

Beside the intensification at a local scale, changes at the level of landscape scale may also affect predators in the agricultural field. Diverse natural or semi-natural habitat adjoining crop field and also a more complex landscape structure can provide refuges or source habitats and are therefore important for the colonisation of fields by predators such as spiders as reviewed by Marc et al. (1999) for several agricultural fields and shown by e.g. Schmidt et al. (2008) in case of wheat fields and by e.g. Schoenly et al. (2010) for paddy fields. However, expanding agricultural land, establishing monocultures and shifting to new crop types at the expenses of natural or semi-natural habitats are common phenomena (Tilman et al., 2001; Laurance, 2010).

In this study we focus on the abundance of spiders, their webs as well as their potential prey in rice fields in South India. Furthermore, landscape structure and cultivation practices were considered. On this basis we seek to answer the following three research questions:

(1) How do prey availability, management practices and landscape structure affect different spider families and spider web types in paddy fields?

(2) Does a spider web survey provide additional information to spider sampling?

(3) Can spider webs be used by the farmers for a quick observational and non-destructive assessment of spider and pest abundance in the field?

Material and Methods

Study site

The study took place in the Wayanad district, Kerala State, South India. Wayanad is an undulating plateau located in the Western Ghats between the Kerala plains in the west and the Mysore plateau in the east. The hilly terrain ranges between 700 and 2100 MSL. The climate is classified as a tropical monsoon climate with a mean temperature range of 18 °C to 29 °C and an annual rainfall of 2,322 mm. Agriculture is the major source of livelihood in Wayanad for the majority of the inhabitants. Most of the agricultural land is maintained by subsistence farmers and small-holder plantations (Santhoshkumar & Ichikawa, 2010). In diverse homegardens on the hill tops, surrounding the farm houses, farmers grow fruit trees, coffee, spices, vegetables, coconut etc. for self-sufficiency (Kumar *et al.,* 2010). However, driven by the market these homegardens are partially transformed into simplified systems such as rubber or coffee plantations. Paddy is cultivated in the plains surrounding the hills and its cultivation in this area is mainly rain fed and therefore usually only one crop per year is possible. Cultivation starts in July after the monsoon rain and ends with the harvest in December. In recent history, the Green Revolution, a most influential intervention in rice cultivation in all Asian countries starting in the mid-1960s, led to intensified rice cultivation by the introduction of chemical fertilisers and pesticides, machinery and improved rice varieties (Settle *et al.* 1996; Pandey *et al.,* 2010). As a consequence of the commercialisation of agriculture in the late 1990s the cultivation of cash crops such as banana, arecanut, ginger and turmeric increased considerably and contributed largely to the foreign exchange earnings of the district (George & Krishnaprasad, 2006). These cash crops are grown in transformed rice fields. Hence the expansion of cash crops resulted in a drastic reduction of the rice cultivation area from 30,000 ha (1980-81) to 8,995 ha (2011-12) (GOI 2013). However, rice cultivation is still continued by several farmers and recently promoted by programmes to cultivate and conserve traditional rice varieties (Manoj, 2012) and by prohibition of conversion of paddy land for other purposes (Government of Kerala, 2008).

Experimental design

In total, 18 rice fields were selected. To incorporate cultivation practices and landscape structure, we selected rice fields with high-intensity and low-intensity management adjacent to homegardens (diverse polycultures) and banana fields (intensified monocultures). Samples were taken in 12 subplots per field each 2 x 1 m in size, 2 m apart from each other. These subplots were located within three transects to cover the different microhabitats constituting a rice field: at the edge of the field, closest to the adjacent habitat, 10 meters into the field and at the earthen bunds in the midst of the rice fields (Fig. 1); the distance from the centre transect to bund transects varied between 5 and 10 meters depending on the field size.

To differentiate between low-intensity and high-intensity fields we interviewed farmers about their cultivation practices during the field site selection. Additionally, management steps were recorded regularly during the whole sample period as farmers were flexible in the management practices they applied. We focused on the three major practices of intensification: the amount of applied fertiliser (min = 14.29 kg/acre; max = 285.71 kg/acre) and whether insecticides were applied and weeding was done or not (Table S1). The information about the amount of insecticide application was too incomplete to be taken into account. No herbicides were used in the study region and weed control was done only manually. Permission to work in their rice fields was provided by the farmers in form of a written agreement.

Figure 1: Paddy fields beside homegarden polyculture (top left) and banana monoculture (top right) and sketch of the experimental design. In total 18 rice fields with high-intensity and low-intensity management were selected. Fields were located either adjacent to homegarden polycultures or banana monocultures. Samples were taken in four subplots (each 2 x 1 m, 2 m apart) within three transects (edge, centre, bund) in each field.

Data collection

The survey took place during the cropping season after the South-West Monsoon, between August and December in 2011 and 2012. Samples were taken once a month; one each during tillering stage of the rice, during panicle initiation and during flowering to cover the different phonological stages of the rice crop. In 2012, an additional sample round during milk ripening stage was conducted, which, however, was not permitted in 2011 by most of the farmers. Samples were taken on predominantly dry days between 8 am and 2 pm in an alternating order so that each field was sampled in the morning as well as at noon time. Spiders and insects were collected by sweep netting, conducting five sweeps per subplot and sampling in 2011 and, as the yield was not as high as expected, 15 in 2012. Sweep netting was always done by LB. Spiders were transferred into separate collecting bottles containing a cotton ball soaked in ethyl acetate whereas all insects were transferred into bottles filled with isopropyl alcohol. Samples were brought to the lab for identification and if possible spiders and plant- and leafhoppers (hereafter referred to as leafhoppers) were identified up to species level, otherwise grouped into morphospecies. All other insects were counted and grouped into orders. All specimens were preserved in 70 % isopropyl alcohol and stored in the collection of the Zoological Survey of India, WGRC Calicut. Identification of spiders was based on Tikader (1987); Barrion & Litsinger (1995); Murphy & Murphy (2000); Proszynski (2003); Jocqué & Dippenaar-Schoeman (2007); Sebastian & Peter (2009) and the taxonomy followed the World Spider Catalog (2014). Leafhopper identification was based on the descriptions given by Kalshoven (1981) and names were cross checked with Encyclopedia of Life (EOL).

Spider webs were surveyed in 2012 during the flowering and milk ripening stages. Each subplot was carefully searched for webs; they were counted and identified. A spray bottle filled with water was used to increase webs' visibility. They were categorised into four sizes: tiny (5-10 cm Ø), small (10-15 cm), medium (15-20 cm) and large (≥ 20 cm), and their direction (horizontal, vertical and diagonal) was noted as was their location (top, middle, at base of the rice tillers, and on the ground/soil). These parameters were not included in the analyses but are closely linked to the web types of Jocqué & Dippenaar-Schoeman (2007) and Sebastian & Peter (2009) which were used for web identification.

A plant survey to assess weed richness and cover in the rice fields was conducted in 2012 during panicel initiation and milk ripening. In each subplot plant species were identified and the coverage for each species was estimated. Specimens that could not be identified in the field were collected and taken to the lab for closer investigation. Sasidharan (2011) and The Plant List (2013) were used as a reference of weed identification and recent taxonomy.

Furthermore, the current landuse in the surrounding of each plot was mapped within a 500m radius based on Googel Earth pictures (scale = 1.7:10,000), verified by a field survey and digitised to a GIS map using ArcGIS 10 (ESRI 2011). We selected a 500m radius which seemed to capture the landscape size relevant to spider dispersal (e.g. Schmidt and Tscharntke 2005). Habitat diversity of each landscape was calculated based on the number of different habitat types and the percentage of each habitat type of the total area of the respective landscape using the Shannon Index (diversity function in the vegan package in R) (Steffan-Dewenter *et al.*, 2002).

Statistical analysis

We pooled the data per transect to get a strong sample basis. We conducted a multivariate analysis using the mvabund package (3.9.3) (Wang *et al.,* 2015) using R (3.1.2) (R Core Team, 2014) to analyse the response of different spider families and spider web types to several environmental and management factors. The mvabund package builds on a model-based approach for the analysis of multivariate abundance data. The function manyglm of the mvabund package computes generalised linear models for each species (or as in our case, families) in a dataset seperately using a collective set of explanatory variables. Using the function anova.manyglm(), adjusted for multiple testing, p.uni = "adjusted", multivariate and univariate results for each family were obtained. Until now manyglm does not accept mixed effects models. We used a negative binomial distribution to account for count data. An inference tool takes correlations between families into account (Wang *et al.,* 2012). Test for homoscedasticity, normality of errors and absence of outliers were done by diagnostic plot of each model.

To check for correlations between the exlanatory variables, namely adjacent habitats (homegarden or banana), amount of applied fertiliser (kg/ acre), insecticide application, weed operations, landscape diversity, abundance of leafhoppers, lepidoptera and other insects, weed richness, percentage of weed cover and the percentages of landscape components (homegarden, banana, paddy and fallow) in the landscape, a Spearman's correlation test was conducted (Tabel S2). Due to correlations between landscape structure and percentace of homegarden, leafhopper abundance and abundance of lepidoptera and other insects respectively, we fitted the following models:

(1) y ~ adjacent habitat + amount of applied fertiliser + insecticide application + weed operations + landscape structure + abundance of all insects + weed richness + percentage of weed cover

(2) y ~ % homegarden + % banana + % paddy + % fallow

(3) y ~ leafhopper abundance

(4) y ~ lepidoptera abundance

(5) y ~ abundance of other insects.

Additionally, to check whether there might be an indirect effect of fertiliser through prey abundance, we conducted a Spearman correlation test between the abundances of planthoppers, Lepidoptera and other insects and fertiliser application.

RESULTS

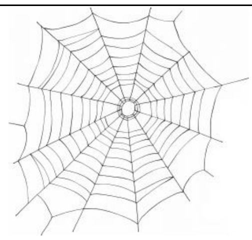
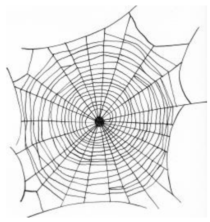
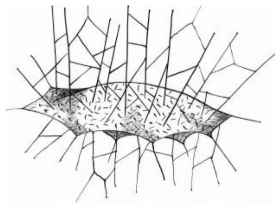
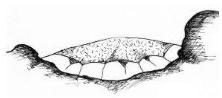
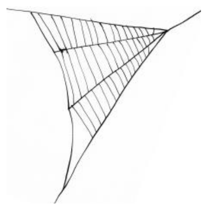
In total, 2073 spider individuals belonging to 15 families and 86 species were collected. Only the seven most abundant spider families were included in the analysis (total abundance ≥ 40), i.e. Tetragnathidae, Oxyopidae, Salticidae, Araneidae, Lycosidae, Linyphiidae, Thomisidae (Table 1 & Table S3). For the other families we had too few counts to obtain meaningful results. A total of 386 spider webs were counted and classified into five different web types, namely orb webs, space webs, ground webs, tetragnathid webs and reduced webs (Table 2). Reduced webs were excluded from the analysis because of insufficient recordings.

A total of 15620 leafhoppers were counted over the two years with 10367 individuals collected in 2012 and identified up to species level. Leafhoppers were dominated by potential rice pest species, namely *Sogatella furcifera* (Horváth) (n=2103), *Nephotettix* spp. (n=1899) and *Recilia dorsalis* Motschulsky (n=573) (Table S4). Furthermore, 7116 insects of ten orders other than leafhoppers were recorded, i.e. Coleoptera, Dermaptera, Hemiptera, Hymenoptera, Isoptera, Lepidoptera, Mantodea, Odonata, Orthoptera and Planipennia (Table S5). Among the 1396 Lepidoptera (adult and larvae) observed we recorded high numbers of *Nymphula depunctalis* Guenée (rice leaf-roller) and *Cnaphalocrocis medinalis* Guenée (leaf-folder) (together constituting about 70 % of the 2012 samples), both known as being common rice pests.

Table 1: Short characterisation of the seven most abundant spider families found in paddy fields in Wayanad, South India. Descriptions are based on Murphy & Murphy (2000); Jocqué & Dippenaar-Schoeman (2007); Sebastian & Peter (2009) and own observations (n = number of specimens collected).

Family	Dominant species or genus	Foraging strategy	Habitat	Location in paddy	Picture
Tetragnathidae (n=1024)	*Tetragnatha* spp. (n=934)	large, horizontal orb webs with open hub	tallish grass and vegetation, wetlands, near water; webs often spanned across streams	paddy canopy	 *Tetragnatha* sp.
Oxyopidae (n=458)	*Oxyopes javanus* (n=164 plus 293 juvenile specimen, most likely *O. javanus* also)	chasing or stalking	grasses, herbs and shrubs	mid height of paddy vegetation	 *Oxyopes javanus*
Salticidae (n=255)	*Carrhotus viduus* (n=139)	stalking or chasing	shrubs, tallish grasses, paddy plants	mid height of paddy vegetation	 *Carrhotus viduus*
Araneidae (n=111)	*Neoscona* spp. (n=48)	vertical orb webs	marshy grasslands	mid height or canopy of paddy	 *Neoscona* sp.
Lycosidae (n=61)	*Pardosa summatrana* (n=31)	free hunting	grassland, damp ground among leaf litter	on ground or water surface of paddy fields, sometimes at the base of paddy tillers	 *Pardosa summatrana*
Linyphiidae (n=60)	*Atypena adelinae* (n=37)	3-dimensional sheet webs	grass fields, lawns	mid or base of paddy tillers	 *Atypena adelinae*
Thomisidae (n=41)	*Thomisus* (n=11)	ambushing (often camouflaged as flowers)	flowers, foliage	mid height of paddy vegetation	 *Thomisus pugilis*

Table 2: Spider web types found in the rice fields and the spider families associated with these web types. Descriptions and family allocations are based on Jocqué & Dippenaar-Schoeman (2007); Sebastian & Peter (2009) and own observations (n = number of webs collected).

Web Guild	**Web description**	**Family/ Genus associated with web type**	**Web location within the paddy vegetation**	**Schematic drawing of the web**
tetragnathid webs (n=192)	large, horizontal orb webs with an open hub	Tetragnathidae	paddy canopy	
orb webs (n=72)	orb webs, different in size, with or without stabilamentum (bands of dense silk)	Araneidae, Theridiosomatidae, Uloboridae (webs of Theridiosomatidae are hoisted in the centre like a tent)	mid height or base of paddy vegetation	
space webs (n=66)	3-dimensional web constructions with or without sheet like structure in the centre	Linyphiidae, Pholicidae, Theridiidae	mainly at the base of paddy tillers	
ground webs (n=48)	tiny sheet webs woven over small pits in the soil or holes created by small stones or balls of earth	*Erigone* spp. (Linyphiidae)	on the ground	
reduced webs (n=8)	triangular webs or reduced orb webs with missing sectors	Uloboridae, *Cyrtarachne* spp. (Araneidae)	mid height of paddy vegetation	

The results of the multivariate analysis (Table 3 & Supp. Information III) showed that adjacent habitat and landscape structure did not affect spider families or spider web types. Furthermore, no effect was found for the three management practices, fertiliser and insecticide application and weeding operation. Weed richness did not affect spider families or web types. Also the percent of different landscape components had no effect on spider families; in case of spider webs only percent of fallows showed an influence as ground webs were positively related to percent of fallows.

Table 3: P-values of the univariate test of the manyglm models for spider families and spider webs. Bold numbers indicate significance. Signif. Codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1. homegarden = percent of homegarden area in the landscape, banana = percent of banana fields, paddy = percent of paddy fields, fallow = percent of fallow fields. Landscape refers to a circle of 500m radius around each sampled rice fields. Insect abundance = abundance of insects except leafhoppers and Lepidoptera.

	Spider families						
Explanatory variables	Tetraganthidae	Oxyopidae	Salticidae	Araneidae	Lycosidae	Linyphiidae	Thomisidae
Adjacent habitat	0.687	0.687	0.839	0.687	0.839	0.764	0.839
Landscape structure	0.995	0.995	0.995	0.983	0.995	0.735	0.967
Amount of fertiliser application	0.721	0.555	0.572	0.372	0.721	0.721	0.721
Insecticide application	0.996	0.95	0.996	0.867	0.989	0.996	0.949
Weeding	0.183	0.99	0.917	0.811	0.917	0.75	0.969
Total insect abundance	**0.002**	**0.012**	0.123	0.072	**0.053**	0.072	0.133
Plant richness	0.741	0.741	0.905	0.592	0.905	0.905	0.858
Percent of herb cover	0.17	0.003	0.288	0.247	0.288	0.24	0.24
Homegarden	0.953	0.905	0.694	0.694	0.905	0.694	0.975
Banana	0.36	0.678	0.698	0.485	0.698	0.698	0.698
Paddy	0.978	0.978	0.848	0.858	0.978	0.714	0.848
Fallow	0.963	0.963	0.963	0.918	0.901	0.829	0.829
Leafhopper abundance	**0.001**	**0.006**	0.301	0.498	0.077	**0.034**	0.301
Lepidoptera abundance	**0.001**	**0.006**	**0.006**	**0.048**	**0.048**	**0.009**	**0.048**
Insect abundance	**0.013**	**0.001**	**0.013**	0.2	0.13	0.2	0.2

	Spider webs			
Explanatory variables	orb webs	tetragnathid webs	space webs	ground webs
Adjacent habitat	0.892	0.535	0.47	0.892
Landscape structure	0.642	0.687	0.302	0.257
Amount of fertiliser application	0.132	0.129	0.129	0.129
Insecticide application	0.347	0.347	0.469	0.95
Weeding	0.974	0.272	0.974	0.655
Total insect abundance	**0.001**	**0.001**	0.628	0.628
Plant richness	0.764	0.764	0.596	0.764
Percent of herb cover	0.32	0.32	0.176	0.32
Homegarden	0.856	0.117	0.856	0.856
Banana	0.985	0.53	0.877	0.169
Paddy	0.827	0.492	0.827	0.526
Fallow	0.333	0.333	0.333	**0.003**
Leafhopper abundance	**0.018**	**0.006**	0.753	0.753
Lepidoptera abundance	**0.014**	**0.001**	0.227	0.989
Insect abundance	**0.001**	**0.001**	0.897	0.897

Spider abundance and spider web number was mainly driven by the number of available insect prey (Fig. 2, Table S6) but a closer look revealed different responses to the abundance of leafhoppers, Lepidoptera and other insects. As the results of the univariate analysis showed, all spider families were positively related to Lepidoptera abundance while only Tetragnathidae, Oxyopidae and Linyphiidae responded positively to leafhopper abundance and Tetragnathidae, Oxyopidae and Salticidae significantly increased with raising numbers of other insects (Fig 3, Tables S8, S9 & S10). Furthermore, an increasing herb cover was negatively related to spider families but result was only significant for Oxyopidae (Fig 2, Table S6).

The analysis of spider webs showed similar results as the analysis of spider families, the abundance of insects being the most important (Fig. 4A, Table S11). Tetraganthid and orb webs increased with numbers of leafhoppers, Lepidoptera and other insects (Fig. 5, Table S13, S14 & S15). Moreover, spider web numbers were positively related to higher percentages of fallow fields in the surrounding landscape (Fig. 4B, Table S12) while herb cover had no effect. Fertiliser applications were not related to planthoppers, Lepidoptera and other insects (Fig. S1).

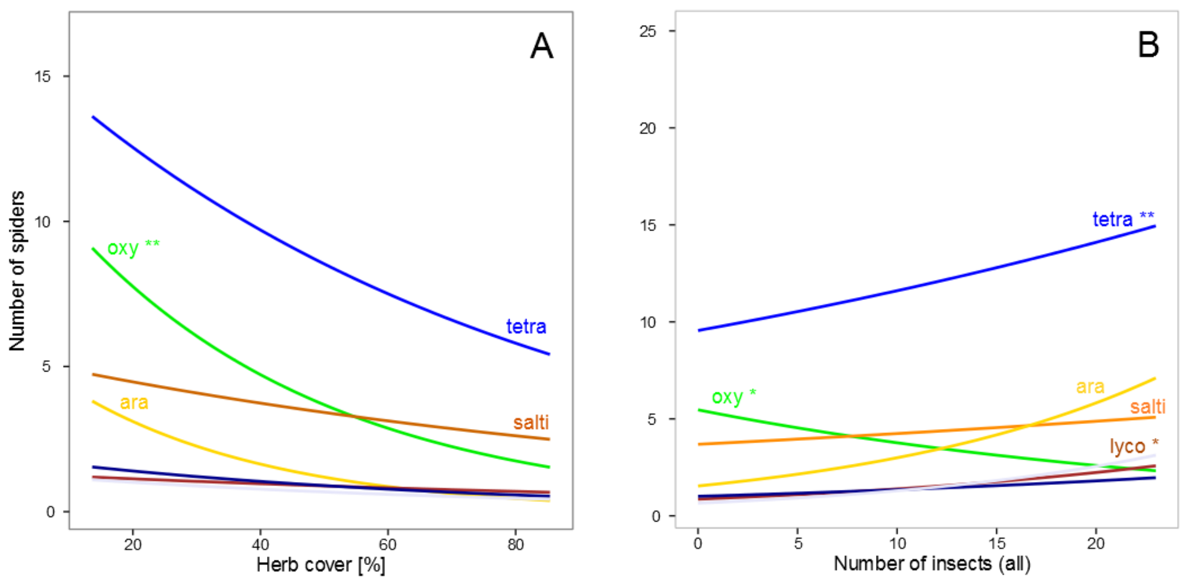


Figure 2: Response of spider families to (A) percent of herb cover in the paddy fields and (B) insects abundance. Significance codes: *** ≤ 0.001; ** ≤ 0.001; * ≤ 0.05; ≤ 0.1. . ara = Araneidae, liny = Linyphiidae, lyco = Lycosidae, oxy = Oxyopidae, tetra = Tetragnathidae, thom = Thomisidae.

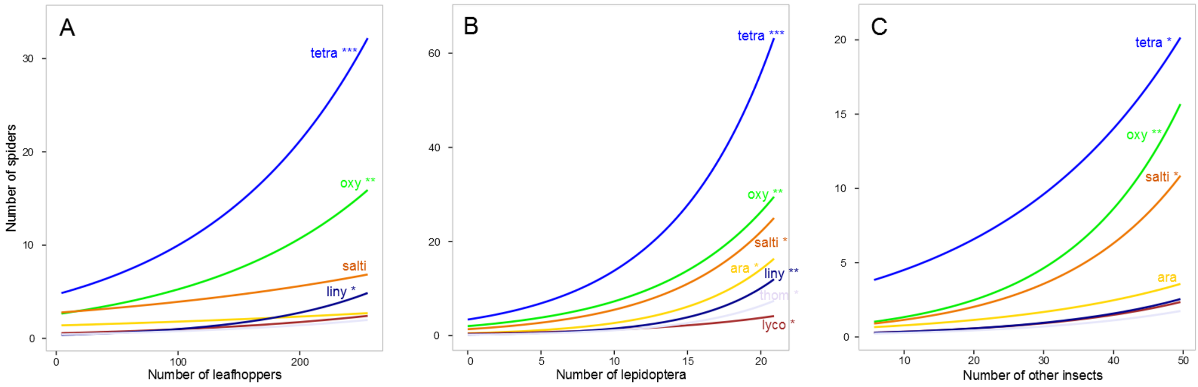


Figure 3: Relationship between spider families and (A) leafhopper abundance, (B) Lepidoptera abundance and (C) other insects except leafhoppers and Lepidoptera. Significance codes: *** ≤ 0.001; ** ≤ 0.001; * ≤ 0.05; ≤ 0.1. ara = Araneidae, liny = Linyphiidae, lyco = Lycosidae, oxy = Oxyopidae, tetra = Tetragnathidae, thom = Thomisidae.

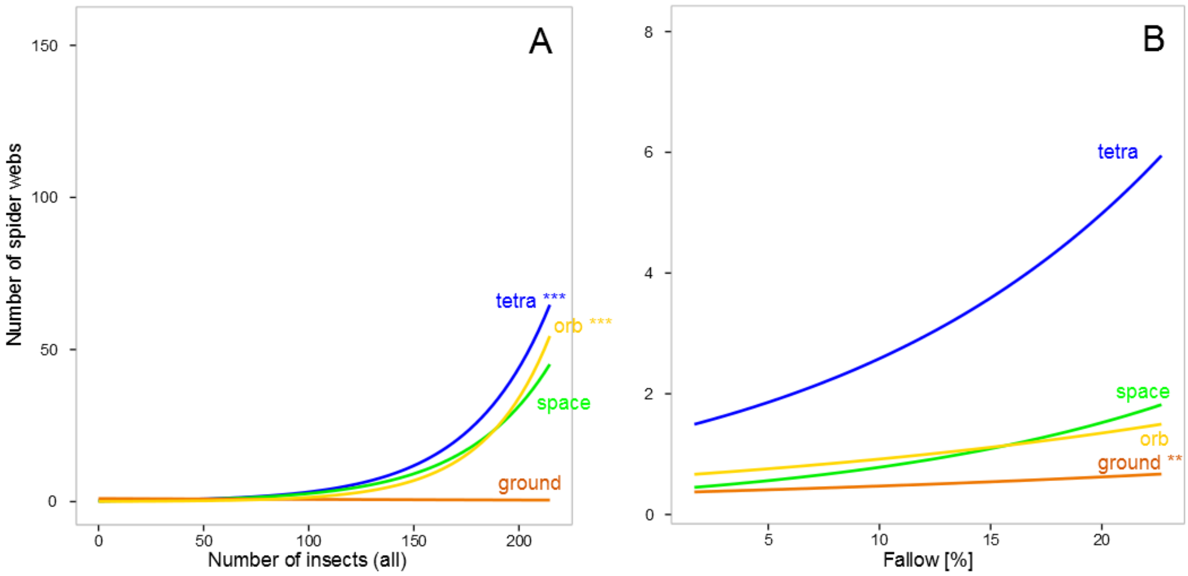


Figure 4: Relationship between spider web types and (A) insect abundance and (B) percentage of fallow field in the surrounding landscape. Significance codes: *** ≤ 0.001; ** ≤ 0.001; * ≤ 0.05; ≤ 0.1. ground = ground webs, orb = orb webs, space = space webs, tetra = Tetragnathidae-webs.

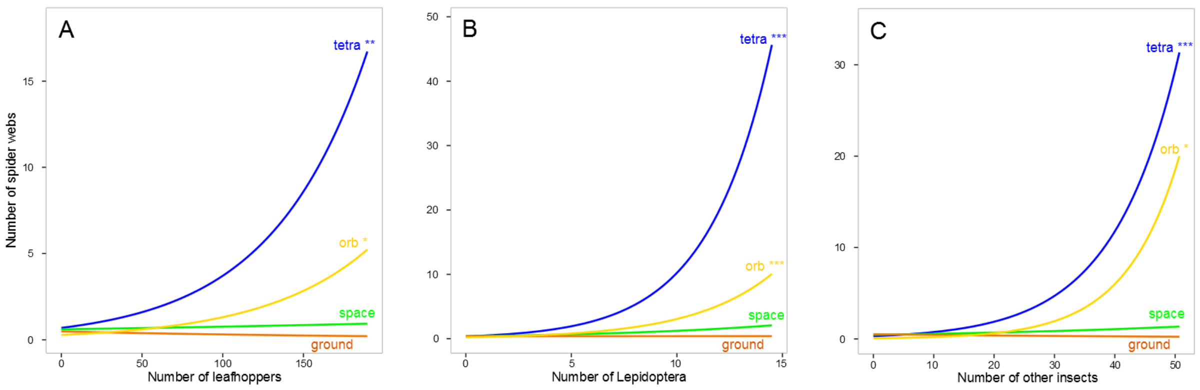


Figure 5: Relationship between spider web types and increasing (A) leafhopper abundance, (B) Lepidoptera leafhopper and (C) other insects except leafhoppers and Lepidoptera. Significance codes: *** ≤ 0.001; ** ≤ 0.001; * ≤ 0.05; ≤ 0.1. ground = ground webs, orb = orb webs, space = space webs, tetra = Tetragnathidae-webs.

Discussion

Spider and spider web sampling in South Indian paddy fields resulted in 86 spider species out of 15 families plus five spider web types. The analysis, including the seven most abundant spider families (> 40 individuals) and four spider web types, showed that the availability of prey was the major determining factor. In general, these findings suggest spiders to be driven by a bottom up effect and do not exert top down effects as argued by Maloney *et al.* (2003). Prey "switching" refers to changing prey preferences as a response to the most abundant prey (Nyffeler *et al.,* 1994a; Riechert & Lawrence, 1997). Furthermore, aggregation in prey rich areas is a possible numerical response to high leafhoppers abundances (Marc *et al.,* 1999; Harwood *et al.,* 2001). A closer look at different families and web types revealed differences in responses to prey types within this general pattern and will be discussed in the following.

Planthoppers, Lepidoptera and other insect prey

For the most abundant spider family, Tetragnathidae, the number of leafhoppers and Lepidoptera was most important. Abundance of other insects also had a positive effect, yet less significant. In case of tetragnathid webs, response to leafhopper abundance was least significant compared to Lepidoptera and other insects. Tetragnathidae build large, horizontal webs in the upper part of the rice vegetation or in its canopy. According to Tahir *et al.*, (2009) the order of prey caught by *Tetragnatha javana* (Thorell, 1890) is Lepidoptera followed by Diptera, Homoptera, Coleoptera, Hymenoptera and Orthoptera which correspond with our findings, showing highest increase of Tetraganthidae with increasing abundance of Lepidoptera and leafhoppers. Kiritani *et al.* (1972) also showed that Tetragnathidae prey efficiently on leafhoppers.

For Araneidae only increasing Lepidoptera abundance showed a slightly significant effect. However, the numbers of orb webs, which are primarily built by Araneidae, not only increased significantly with numbers of Lepidoptera but with leafhoppers and other insects as well. Tahir *et al.*, (2009) found that Lepidoptera were the preferred prey of the Araneidae *Neoscona theis* (Walckenaer 1842), which correspond with our findings for Araneidae and orb webs.

Linyphiidae were captured in rather low numbers in this study. This might be partly due to a sample bias. Linyphiidae are usually found at the base of the rice tillers where it was difficult to reach with the sweep net in tall rice varieties (up to 1.4 m high). However, Sebastian *et al.* (2005) recorded similar low numbers of Linyphiidae. Nevertheless, the results showed a slight positive relationship between Linyphiidae and Lepidoptera as well as leafhopper abundance. These findings are in line with Lou *et al.,* (2013) who reported that the Linyphiidae species *Ummeliata insecticeps* (Bösenberg & Strand) do feed on leafhoppers but are more important predators of young Lepidoptera larvae and rice aphids. More than 60% of the captured Lepidoptera in our study were larvae which may explain the positive relation between Lepidoptera and Linyphiidae. The lack of rice aphids in the studied fields could be one reason why abundance of other insects did not have a significant effect.

The second most abundant spider family, Oxyopidae, hunts by chasing or stalking. Oxyopidae increased with abundance of leafhoppers, Lepidoptera and other insects. Tahir & Butt (2009) showed in their experiment that *Oxyopes javanus* Thorell fed on leafhoppers, Lepidoptera and grasshopper nymphs but preferred Lepidoptera larvae over leafhoppers nymphs and adults. Least favourite were grasshopper nymphs. Noticeable were the high numbers of immature *Oxyopes* individuals. Barrion *et al.* (2012) found such high number of immature *Oxyopes* in rice fields in China as well and reported their efficiency in feeding on nymphs of leafhoppers.

Salticidae, also hunting spider, increased with higher numbers of Lepidoptera and other insects. The frequently observed moth *N. depuntalis* and *C. medinalis* fit into the prey spectrum of *Carrhotus viduus* (C. L. Koch) Sebastian & Peter (2009), which was the dominating Salticidae. Additionally, Salticidae may prey on the larvae of *N. depunctalis* and *C. medinalis* which were mostly observed in the middle layer of the rice vegetation, the preferred hunting ground of Salticidae. Furthermore, Salticidae may also hunt less airworthy insects such as beetles (Riechert & Bishop, 1990, Nyffeler *et al.*, 1994b) which could explain their positive response with other insects.

The numbers of Lycosidae found in this study was comparatively low most likely due to sweep net sampling only. Pitfall traps would have been the more appropriate device for sampling ground running spiders but due to standing water in the field they could not be installed. In contrast to studies by Kiritani *et al.*, 1972, Nyffeler & Benz (1987), and Lou *et al.*, 2013 who reported leafhoppers to be the preferred prey of Lycosidae, our results indicated an increase in Lycosidae abundance with higher numbers of Lepidoptera. However, the analysis showed a slight positive response to leafhopper abundance as well, yet not significant. Most likely this result is owed to the low individual numbers of Lycosidae.

Weed cover and richness

Structural diversity was hypothesised to be important for spiders as it provides hiding places for hunting spiders and diverse options for web builders to fix their webs and furthermore, additional prey insects which are related to non-crop plants (Balfour & Rypstra 1998, Sunderland & Samu 2000, Foelix, 2011). However, we did not find any effects of plant diversity on spider families nor on spider webs. Moreover, our results showed a decline in abundance for all spider families with increasing herb cover in the rice fields. However, only the effects on Oxyopidae were significant. Probably too dense vegetation impedes foraging of this free hunting spiders and thus the prey had more options to hide (Butt & Xaaceph, 2015) or the chance that prey was intercepted by spider webs was lower in these more dense vegetation. Web builders need enough structure to fix their webs but also require enough space to build them properly (Foelix, 2011).

Adjacent habitat and management

In contrast to the findings of Clough et al. (2005) and Schmidt et al. (2008), no effect was found for the type of adjacent habitat (homegarden polyculture vs banana monoculture) or for landscape structure. Only the percentage of fallow fields in the surrounding showed a positive impact on the number of ground webs. Fallows serve as overwintering sites for some spiders, especially those living in small crevice of the soil and on the bunds (Arida & Heon, 1994, Bambaradeniya et al., 2004). This might be one explanation for the correlation of ground webs and fallows. One explanation might be that the most abundant spider families are well adapted to the rice agroecosystem and can cope with its frequent disturbances (Way & Heong, 1994; Bambaradeniya et al., 2004). Hence the type of adjacent habitat and landscape structure appeared to be of less importance for these families.

Several studies showed a harmful effect of chemical insecticides and fertilisers on spiders (e.g. Marc et al., 1999; Settle et al., 1996; Amano et al., 2011). However, we did not find any effect of fertiliser or insecticide application. Insect abundance too was not affected by fertiliser application suggesting no indirect effect through prey abundance. The reason for the lacking impact of management could be that intensification of rice cultivation in the studied region did not yet reached levels high enough to significantly damage the spider population (Zhao et al.

2015b). Compared to other rice cultivation regions, the intensification observed in Wayanad is very modest (Lu & Heong, 2009).

Spider web sampling

Although the identification of spider webs was not so easy and perhaps less precise compared with studies by Gollan et al. (2010) and Stenchly et al. (2011) conducted in woody habitats, the diverging results for orb webs vs. Araneidae and ground webs (*Erigone* spp. Linyphiidae) and Linyphiidae suggested that spider web sampling can give useful additional information to spider sampling. The analysis of spider families only showed an increase of Araneidae with an increasing number of Lepidoptera while the analysis of spider webs indicated that orb webs, which are mainly woven by Araneidae, responded positively to increasing numbers of leafhoppers and also other insects. Ground webs, which are tiny, sheet webs woven by Erigoninae (Linyphiidae) over small holes in the soil were positively related to higher percentages of fallows in the surrounding, but this effect was not found for Linyphiidae. In fields where pitfall traps are impossible to install, the survey of spider webs might be a good addition to sweep netting, as it is rather difficult to catch these tiny spiders at the base of the rice tillers especially in later cropping stages when the crop is grown high. The same may apply for Araneidae, which hide in the middle layer of the vegetation. In addition, the large horizontal webs built by Tetragnathidae in the rice canopy are easy to observe in the early morning when covered with dew drops. Since both, the number of tetragnathid webs and numbers of Tetragnathidae increased with the abundance of leafhoppers in the field, high numbers of tetragnathid webs could be an indicator for the local farmers to check their fields for possibly harmful infestations of leafhoppers.

CONCLUSION

In conclusion, the findings of this study showed that the major determining factor for overall spider and spider web abundance was the prey availability, suggesting that the spider community in these paddy fields was driven by bottom up effects. A closer look at different families and web types revealed some differences within this general pattern.

For the web building Tetragnathidae and Linyphiidae Lepidoptera and leafhopper abundance were most important while Araneidae responded to Lepidoptera. The hunting spider Oxyopidae responded positively to Lepidoptera, leafhoppers and other insects. For this family we also found a slight negative effect of increasing herb cover in the paddy fields. The number of Salticidae and Lycosidae, also a hunting spider, were only correlated with increasing numbers of

Lepidoptera. However, the low number of Lycosidae, presumably due to a sampling bias, may affect the result of the analysis.

The lacking effect of adjacent habitat type (homegarden polyculture vs banana monoculture) and landscape structure may suggest that the contrast between the selected habitats and between the landscapes were not strong or relevant enough for the most abundant spider families. Further, the considered spider families are possibly very well adapted to the rice agroecosystem and can cope with its frequent disturbances. Only the percent of fallow fields in the surrounding of the fields showed an effect on ground webs, build by Erigoninae (Linyphiidae). Additionally, fertiliser and insecticide application did not play an important role, suggesting that the level of intensification in the study region did not reach a critical point, yet.

Diverging results for web and spider abundances suggest that spider web sampling can be a useful complement to spider sampling. In addition, large numbers of tetragnathid webs are easy to observe and may be a helpful indicator for farmers to survey their fields for possibly harmful infestation with rice pests.

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APPENDIX

Table S1: Average values for each management practice.

management practice	high intensity paddy	low intensity paddy	adjacent home-garden	adjacent banana field
fertiliser application [kg/ acre]	134.52	51.92	102.15	84.29
insecticide application [yes or no]	0.78	0.22	0.67	0.33
Weeding [yes or no]	0.56	0.22	0.44	0.33

Table S2: Before the data analysis we conducted a Spearman's correlation test containing all explanatory variables.

>	cor(cbind(hab,ferti,pesti,weed,LSC,cic.abu,ins.abu2,lepi,plants,herb.cov,homegarden,banana,paddy,fallow),method="spearman")													
	hab	**ferti**	**pesti**	**weed**	**LSC**	**cic.abu**	**ins.abu2**	**lepi**	**plants**	**herb.cov**	**homegarden**	**banana**	**paddy**	**fallow**
hab	1	0.06448259	0.33333333	0.11396058	0.33246955	-0.28397739	-0.11288019	0.02616912	-0.25137491	-0.08079845	-0.33930735	-0.06789656	-0.23930098	0.51074686
ferti	0.06448259	1	0.42988392	0.3527267	0.077801	-0.07975888	0.10682607	0.09796814	0.20649579	-0.07183033	-0.17065945	0.04026742	0.45048567	0.17964152
pesti	0.33333333	0.42988392	1	-0.11396058	0.3968185	0.03802208	0.13783266	0.1700993	-0.12151773	0.13070338	-0.35359398	-0.05360255	0.48217361	0.48217361
weed	0.11396058	0.3527267	-0.11396058	1	-0.12099851	0.18401785	-0.0158429	0.23668207	0.15640354	0.00853079	-0.0769283	-0.40683123	0.03296927	-0.18682586
LSC	0.33246955	0.077801	0.3968185	-0.12099851	1	-0.18711372	-0.02138975	-0.04460568	-0.07014585	0.22588262	-0.69294444	-0.04863467	-0.07032869	0.31027363
cic.abu	-0.28397739	-0.07975888	0.03802208	0.18401785	-0.18711372	1	0.63828692	0.66996797	-0.27997958	0.09876684	0.07468886	-0.28584074	0.15986205	-0.17895918
ins.abu2	-0.11288019	0.10682607	0.13783266	-0.0158429	-0.02138975	0.63828692	1	0.33017249	-0.27297144	0.05817101	0.05372124	-0.23081698	-0.05589836	0.10944772
lepi	0.02616912	0.09796814	0.1700993	0.23668207	-0.04460568	0.66996797	0.33017249	1	-0.16083507	-0.02524377	-0.05209729	-0.17362629	0.24687426	0.04945897
plants	-0.25137491	0.20649579	-0.12151773	0.15640354	-0.07014585	-0.27997958	-0.27297144	-0.16083507	1	0.11598038	0.28067024	0.04643856	0.06100528	-0.15831502
herb.cov	-0.08079845	-0.07183033	0.13070338	0.00853079	0.22588262	0.09876684	0.05817101	-0.02524377	0.11598038	1	-0.18010844	-0.06727703	0.1560456	0.03794672
homegarden	-0.33930735	-0.17065945	-0.35359398	-0.0769283	-0.69294444	0.07468886	0.05372124	-0.05209729	0.28067024	-0.18010844	1	0.21193501	-0.31389208	-0.50424799
banana	-0.06789656	0.04026742	-0.05360255	-0.40683123	-0.04863467	-0.28584074	-0.23081698	-0.17362629	0.04643856	-0.06727703	0.21193501	1	0.08580783	-0.06122567
paddy	-0.23930098	0.45048567	0.48217361	0.03296927	-0.07032869	0.15986205	-0.05589836	0.24687426	0.06100528	0.1560456	-0.31389208	0.08580783	1	0.15086108
fallow	0.51074686	0.17964152	0.48217361	-0.18682586	0.31027363	-0.17895918	0.10944772	0.04945897	-0.15831502	0.03794672	-0.50424799	-0.06122567	0.15086108	1
# correlations between LSC/homegarden cic.abu/ins.abu2 cic.abu/lepi														
# new variable combining cic.abu and ins.abu: ins.abu.all														

Table S3: Spiders species collected in 18 rice fields in Wayanad, South India from August till December in 2011 and 2012.

Species	# Individuals	Guild
Sp. 1	2	
n.i.	27	
Araneidae	**111**	orb weaver
Araneus ellipticus (Tikader & Bal, 1981)	15	
Araneus n.i.	5	
Araneus sp. 14	2	
Argiope aemula	1	
Argiope catenulata (Walckenaer, 1841)	1	
Argiope sp.	1	
Argiope sp. 2	1	
Argiope sp. 8	1	
Cyrtarachne sp. 13	1	
Cyrtophora cicatrosa (Stoliczka, 1869)	1	
Cyrtophora sp. 19	1	
Cyrtophora sp. 21	1	
Cyrtophora sp. 4	1	
Eriovixia laglaizei (Simon, 1877)	2	
Gea sp.	1	
Larinia phthisica (L. Koch, 1871)	8	
Neoscona sp.	48	
Neoscona sp. 6	2	
Ordgarius sp.	3	
n.i.	15	
Clubionidae	**12**	foliage runner
Clubiona sp.	11	
n.i.	1	
Corinnidae	**2**	ground runner
Castianeira zetes Simon, 1897	1	
Corinnomma sp. 1	1	
Linyphiidae	**60**	space web builder
Atypena adelinae Barrion & Litsinger, 1995	37	
sp. 4	2	
n.i.	21	
Lycosidae	**61**	ground runner
Pardosa heterophthalma (Simon, 1898)	1	
Pardosa pseudoannulata (Bösenberg & Strand, 1906)	2	
Pardosa sumatrana (Thorell, 1890)	31	
Pardosa sp. 1	2	
Pardosa sp.	19	
n.i.	6	
Oxyopidae	**458**	stalker
Oxyopes birmanicus Thorell, 1887	1	
Oxyopes javanus Thorell, 1887	164	

Oxyopes sp.	293	
Philodromidae	**2**	ambusher
Philodromus	1	
n.i.	1	
Pholcidae	**1**	space web builder
Pisauridae	**4**	ambusher
Nilus albocinctus (Doleschall, 1859)	2	
Perenethis venusta L. Koch, 1878	1	
Pisaura	1	
Salticidae	**255**	stalker
Bianor	6	
Bianor sp. 1	1	
Bianor sp. 11	3	
Bianor sp. 14	5	
Bianor sp. 2	20	
Bianor sp. 20	1	
Bianor sp. 28	1	
Bianor sp. 3	2	
Bianor sp. 5	3	
Bianor sp. 6	12	
Bianor sp. 7	6	
Carrhotus sp. 12	1	
Carrhotus sp. 16	1	
Carrhotus sp. 21	2	
Carrhotus viduus (C. L. Koch, 1846)	139	
Chalcotropis pennata Simon, 1902	1	
Epeus indicus Prószyński, 1992	3	
Harmochius brachiatus (Thorell, 1877)	13	
Hylleae sp. 24	1	
Myrmarachne orientales Tikader, 1973	1	
Phintella sp. 15	5	
Plexippus sp. 25	1	
sp. 23	1	
sp. 26	3	
sp. 27	1	
sp. 29	1	
sp. 30	1	
sp. 31	1	
sp. 33	1	
n.i.	18	
Tetragnathidae	**1024**	orb weavers
Leucauge decorata (Blackwall, 1864)	1	
Leucauge	3	
Tetragnatha ceylonica O. Pickard-Cambridge, 1869	59	
Tetragnatha javana (Thorell, 1890)	55	
Tetragnatha mandibulata Walckenaer, 1841	4	
Tetragnatha maxillosa Thorell, 1895	236	

Tetragnatha sp.	575	
Tetragnatha sp. 14	1	
Tetragnatha sp. 5	1	
Tetragnatha virescens Okuma, 1979	3	
Tylorida	6	
Tylorida striata (Thorell, 1877)	47	
Tylorida ventralis (Thorell, 1877)	4	
Tylorida xavieri Jose, 2005	2	
Tylorida culta (O. Pickard-Cambridge, 1869)	1	
sp. 15	1	
n.i.	25	
Theridiidae	**11**	space web builder
Achaearanea	1	
Argyrodes sp. 1	1	
Chrysso	1	
Enoplognatha	4	
Phycosoma martinae (Roberts, 1983)	1	
Theridion	1	
Theridula angula (Tikader, 1970)	1	
n.i.	1	
Theridiosomatidae	**1**	orb weaver
Wendilgarda sp.	1	
Thomisidae	**41**	ambusher
Carmaricus formosus Thorell, 1887	1	
Henriksenia hilaris (Thorell, 1877)	9	
Misumena	3	
Misumena sp. 15	2	
Oxytate sp. 3	1	
Oxytate *virens* (Thorell, 1891)	2	
Thomisus lobosus Tikader, 1965	1	
Thomisus	3	
Thomisus pugilis Stoliczka, 1869	6	
Thomisus sp. 1	3	
Thomisus sp. 2	1	
Tmarus sp. 10	2	
Xysticus sp. 18	1	
Xysticus sp. 9	1	
sp. 12	1	
n.i.	4	
Uloboridae	**1**	orb weaver
Zosis geniculata (Olivier, 1789)	1	

Table S4 Plant- and leafhoppers collected in 2011 and 2012 in 18 paddy fields in Wayanad, South India.

Planthoppers 2011	**# Individuals**
Auchenorrhyncha (nymphe)	5253 (1531)
Planthoppers 2012	
Species	**# Individuals**
Aphrophoridae	**3**
Cercopidae	**13**
Cicadellidae	**5484**
Nephotettix	2
Nephotettix nigropictus (Stål, 1870)	1109
Nephotettix virescens (Distant 1908)	788
Recilia dorsalis Motschulsky 1859	573
chocolate brown	2
green	27
light green	548
transparant	827
white	4
yellow head	1417
n.i.	187
Cixiidae	**1**
Delphacidae	**2408**
Nilaparvata lugens (Stål, 1854)	266
Sogatella furcifera (Horváth, 1899)	2103
n.i.	39
Dictyopharidae	**9**
Fulgoromorpha	**1**
Issidae	**340**
Tettigometridae	**1**
nymphe	**2107**

Table S5 Individual numbers of 10 insect orders captured in 18 rice fields in Wayanad South India in 2011 and 2012.

Order	**# Individuals**
Coleoptera	1266
Dermaptera	2
Hemiptera	912
Hymenoptera	732
Isoptera	1
Lepidoptera (larvae)	1396 (886)
Mantodea	1
Odonata	367
Orthoptera	2411
Planipennia	2
n.i.	26

Table S6: Results multivariate and univariate tests of manyglm function with spider families (model (1)).Results were obtained using the function anova.manyglm(), adjusted for multiple testing, p.uni = "adjusted"

Multivariate test:

	Res.Df	Df.diff	Dev	Pr(>Dev)	
(Intercept)	53				
hab	52	1	3,72	0,379	
LSC	51	1	1,31	0,874	
ferti	50	1	5,99	0,191	
pesti	49	1	1,5	0,896	
weed	48	1	4,99	0,337	
ins.abu.all	47	1	38,96	0,001	***
plants	46	1	5,39	0,43	
herb.cov	45	1	25,12	0,002	**

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Univariate tests:

	tetraganthidae		oxyopidae		salticidae		araneidae		lycosidae		linyphiidae		thomisidae	
	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)
(Intercept)														
hab	0,93	0,687	0,896	0,687	0,225	0,839	0,853	0,687	0,261	0,839	0,514	0,764	0,043	0,839
LSC	0,039	0,995	0,008	0,995	0,008	0,995	0,14	0,983	0,023	0,995	0,826	0,735	0,263	0,967
ferti	0,113	0,721	1,268	0,555	1,044	0,572	1,899	0,372	0,62	0,721	0,578	0,721	0,467	0,721
pesti	0,025	0,996	0,32	0,95	0,019	0,996	0,68	0,867	0,09	0,989	0	0,996	0,368	0,949
weed	3,07	0,183	0	0,99	0,186	0,917	0,572	0,811	0,271	0,917	0,855	0,75	0,031	0,969
ins.abu.all	13,825	0,002	8,349	0,012	2,409	0,123	3,531	0,072	5,123	0,053	4,126	0,072	1,595	0,133
plants	1,247	0,741	1,248	0,741	0,186	0,905	1,824	0,592	0,276	0,905	0,015	0,905	0,595	0,858
herb.cov	3,811	0,17	9,949	0,003	1,585	0,288	2,346	0,247	1,223	0,288	3,284	0,24	2,925	0,24

Arguments:

Test statistics calculated assuming uncorrelated response (for faster computation)

P-value calculated using 999 resampling iterations via pit.trap resampling (to account for correlation in testing.

hab = adjacent habitat, LSC = landscape structure, ferti = amount of fertiliser application, pesti = insecticide application, weed = weeding operation, ins.abu.all = total insect abundance, plants = plant species richness, herb.cov = % of herb cover

Table S7: Results multivariate and univariate tests of manyglm function with spider families (model (2)).Results were obtained using the function anova.manyglm(), adjusted for multiple testing, p.uni = "adjusted"

Multivariate test:

	Res.Df	Df.diff	Dev	Pr(>Dev)
(Intercept)	53			
homegarden	52	1	3,041	0,491
banana	51	1	5,915	0,187
paddy	50	1	2,438	0,681
fallow	49	1	2,158	0,764

Univariate tests:

	tetraganthidae		**oxyopidae**		**salticidae**		**araneidae**		**lycosidae**		**linyphiidae**		**thomisidae**	
	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)
(Intercept)														
homegarden	0,035	0,953	0,259	0,905	0,761	0,694	0,834	0,694	0,253	0,905	0,899	0,694	0,001	0,975
banana	1,933	0,36	0,833	0,678	0,57	0,698	1,422	0,485	0,37	0,698	0,645	0,698	0,142	0,698
paddy	0,039	0,978	0,066	0,978	0,461	0,848	0,369	0,858	0,02	0,978	0,939	0,714	0,543	0,848
fallow	0,006	0,963	0,04	0,963	0,09	0,963	0,223	0,918	0,365	0,901	0,669	0,829	0,764	0,829

Arguments:

Test statistics calculated assuming uncorrelated response (for faster computation)

P-value calculated using 999 resampling iterations via pit.trap resampling (to account for correlation in testing.

homegarden = percent of homegarden area in the landscape, banana = percent of banana fields, paddy = percent of paddy fields, fallow = percent of fallow fields. Landscape refers to a circle of 500m radius around each sampled rice fields.

Table S8: Results multivariate and univariate tests of manyglm function with spider families (model (3)).Results were obtained using the function anova.manyglm(), adjusted for multiple testing, p.uni = "adjusted"

Multivariate test:

	Res.Df	Df.diff	Dev	Pr(>Dev)	
(Intercept)	53				
cic.abu	52	1	26,28	0,001	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Univariate tests:

	tetraganthidae		**oxyopidae**		**salticidae**		**araneidae**		**lycosidae**		**linyphiidae**		**thomisidae**	
	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)
(Intercept)														
cic.abu	11,188	0,001	6,486	0,006	1,13	0,301	0,233	0,498	2,577	0,077	3,555	0,034	1,111	0,301

Arguments:

Test statistics calculated assuming uncorrelated response (for faster computation)

P-value calculated using 999 resampling iterations via pit.trap resampling (to account for correlation in testing.

cic.abu = leafhopper abundance

Table S9: Results multivariate and univariate tests of manyglm function with spider families (model (4)).Results were obtained using the function anova.manyglm(), adjusted for multiple testing, p.uni = "adjusted"

Multivariate test:

	Res.Df	Df.diff	Dev	Pr(>Dev)	
(Intercept)	53				
lepi	52	1	40,84	0,001	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Univariate tests:

	tetraganthidae		oxyopidae		salticidae		araneidae		lycosidae		linyphiidae		thomisidae	
	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)
(Intercept)														
lepi	15,137	0,001	6,403	0,006	5,831	0,006	2,798	0,048	2,987	0,048	5,191	0,009	2,494	0,048

Arguments:

Test statistics calculated assuming uncorrelated response (for faster computation)

P-value calculated using 999 resampling iterations via pit.trap resampling (to account for correlation in testing.

lepi = Lepidoptera abundance

Table S10: Results multivariate and univariate tests of manyglm function with spider families (model (5)).Results were obtained using the function anova.manyglm(), adjusted for multiple testing, p.uni = "adjusted"

Multivariate test:

	Res.Df	Df.diff	Dev	Pr(>Dev)	
(Intercept)	53				
ins.abu2	52	1	27,97	0,001	***

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Univariate tests:

	tetraganthidae		oxyopidae		salticidae		araneidae		lycosidae		linyphiidae		thomisidae	
	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)
(Intercept)														
ins.abu2	5,389	0,013	11,064	0,001	5,171	0,013	1,206	0,2	2,177	0,13	1,534	0,2	1,427	0,2

Arguments:

Test statistics calculated assuming uncorrelated response (for faster computation)

P-value calculated using 999 resampling iterations via pit.trap resampling (to account for correlation in testing.

ins.abu2 = abundance of all insects except leafhoppers and Lepidoptera

Table S11: Results multivariate and univariate tests of manyglm function with spider webs (model (1)).Results were obtained using the function anova.manyglm(), adjusted for multiple testing, p.uni = "adjusted"

Multivariate test:

	Res.Df	Df.diff	Dev	Pr(>Dev)	
(Intercept)	49				
hab	48	1	1,78	0,437	
LSC	47	1	3,37	0,218	
ferti	46	1	10,29	0,03	*
pesti	45	1	4,73	0,202	
weed	44	1	3,65	0,35	
ins.abu.all	43	1	31,98	0,001	***
plants	42	1	2,98	0,554	
herb.cov	41	1	14,64	0,131	

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Univariate tests:

	orb webs		**tetragnathid webs**		**space webs**		**ground webs**	
	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)
(Intercept)								
hab	0,082	0,892	0,65	0,535	0,988	0,47	0,058	0,892
LSC	0,281	0,642	0,083	0,687	1,234	0,302	1,767	0,257
ferti	1,677	0,132	2,162	0,129	3,274	0,129	3,177	0,129
pesti	2,007	0,347	1,737	0,347	0,984	0,469	0,006	0,95
weed	0,032	0,974	2,636	0,272	0,036	0,974	0,948	0,655
ins.abu.all	14,841	0,001	15,916	0,001	0,681	0,628	0,54	0,628
plants	0,754	0,764	0,446	0,764	1,582	0,596	0,193	0,764
herb.cov	2,782	0,32	2,891	0,32	6,525	0,176	2,445	0,32

Arguments:

Test statistics calculated assuming uncorrelated response (for faster computation)

P-value calculated using 999 resampling iterations via pit.trap resampling (to account for correlation in testing.

hab = adjacent habitat, LSC = landscape structure, ferti = amount of fertiliser application, pesti = insecticide application, weed = weeding operation, ins.abu.all = total insect abundance, plants = plant species richness, herb.cov = % of herb cover

Table S12 Results multivariate and univariate tests of manyglm function with spider webs (model (2)).Results were obtained using the function anova.manyglm(), adjusted for multiple testing, p.uni = "adjusted"

Multivariate test:

	Res.Df	Df.diff	Dev	Pr(>Dev)	
(Intercept)	49				
homegarden	48	1	2,621	0,268	
banana	47	1	3,169	0,246	
paddy	46	1	2,698	0,403	
fallow	45	1	16,32	0,008	**

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Univariate tests:

	orb webs		tetragnathid webs		space webs		ground webs	
	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)
(Intercept)								
homegarden	0,045	0,856	2,203	0,117	0,162	0,856	0,212	0,856
banana	0	0,985	0,722	0,53	0,103	0,877	2,344	0,169
paddy	0,082	0,827	1,321	0,492	0,203	0,827	1,091	0,526
fallow	1,485	0,333	0,68	0,333	1,624	0,333	12,531	0,003

Arguments:

Test statistics calculated assuming uncorrelated response (for faster computation)

P-value calculated using 999 resampling iterations via pit.trap resampling (to account for correlation in testing.

homegarden = percent of homegarden area in the landscape, banana = percent of banana fields, paddy = percent of paddy fields, fallow = percent of fallow fields. Landscape refers to a circle of 500m radius around each sampled rice fields.

Table S13 Results multivariate and univariate tests of manyglm function with spider webs (model (3)).Results were obtained using the function anova.manyglm(), adjusted for multiple testing, p.uni = "adjusted"

Multivariate test:

	Res.Df	Df.diff	Dev	Pr(>Dev)	
(Intercept)	49				
cic.abu	48	1	13,27	0,006	**

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Univariate tests:

	orb webs		**tetragnathid webs**		**space webs**		**ground webs**	
	Dev	**Pr(>Dev)**	**Dev**	**Pr(>Dev)**	**Dev**	**Pr(>Dev)**	**Dev**	**Pr(>Dev)**
(Intercept)								
cic.abu	5,37	0,018	7,641	0,006	0,055	0,753	0,206	0,753

Arguments:

Test statistics calculated assuming uncorrelated response (for faster computation)

P-value calculated using 999 resampling iterations via pit.trap resampling (to account for correlation in testing.

cic.abu = leafhopper abundance

Table S14 Results multivariate and univariate tests of manyglm function with spider webs (model (4)).Results were obtained using the function anova.manyglm(), adjusted for multiple testing, p.uni = "adjusted"

Multivariate test:

	Res.Df	Df.diff	Dev	Pr(>Dev)	
(Intercept)	49				
lepi	48	1	20,22	0,001	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Univariate tests:

	orb webs		**tetragnathid webs**		**space webs**		**ground webs**	
	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)
(Intercept)								
lepi	5,354	0,014	13,652	0,001	1,216	0,227	0	0,989

Arguments:

Test statistics calculated assuming uncorrelated response (for faster computation)

P-value calculated using 999 resampling iterations via pit.trap resampling (to account for correlation in testing.

lepi = Lepidoptera

Table S15 Results multivariate and univariate tests of manyglm function with spider webs (model (5)).Results were obtained using the function anova.manyglm(), adjusted for multiple testing, p.uni = "adjusted"

Multivariate test:

	Res.Df	Df.diff	Dev	Pr(>Dev)	
(Intercept)	49				
ins.abu2	48	1	15,56	0,001	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Univariate tests:

	orb webs		tetragnathid webs		space webs		ground webs	
	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)
(Intercept)								
ins.abu2	8,261	0,001	7,132	0,001	0,087	0,897	0,082	0,897

Arguments:

Test statistics calculated assuming uncorrelated response (for faster computation)

P-value calculated using 999 resampling iterations via pit.trap resampling (to account for correlation in testing.

ins.abu2 = abundance of all insects except leafhoppers and Lepidoptera

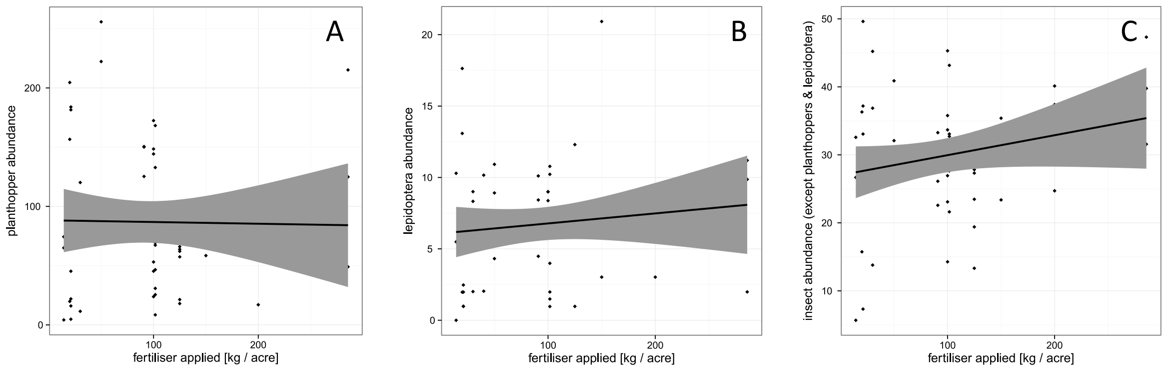

Figure S1: Response of (A) planthoppers (Spearman's rank correlation coefficient (rho) = - 0.080, P = 0.566); (B) Lepidoptera (rho= 0.098, P = 0.481) and (C) other insects (rho = 0.107, P = 0.442) to fertiliser application.

Chapter 3

THE SOCIAL-ECOLOGICAL WEB: A BRIDGING CONCEPT FOR TRANSDISCIPLINARY RESEARCH

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ABSTRACT

Conducting inter-and transdisciplinary research requires integrative tools. This study aims at a better understanding of social-ecological transformation processes through the lenses of indigenous women and men farmers from three different farmer communities in Kerala, South India. Central to the interdisciplinary data analysis is the development of a social-ecological web understood as a bridging concept that seeks to integrate knowledge from social and natural sciences. The social-ecological web is a useful method to highlight differences between the communities, to foster interdisciplinary analysis of both social and ecological changes, and to reflect on the challenges of integrating several disciplines and stakeholders.

INTRODUCTION

In this design report, we reflect on the challenge of integrating social and natural sciences during the research process and propose an innovative tool for interdisciplinary integration which we call a social-ecological web. The development of this web is the output of a social-ecological study conducted as a baseline study in Wayanad district, Kerala, South India. The study is based on an interdisciplinary research programme that looks into social-ecological changes occurring amongst agrarian communities in Wayanad. The rural agricultural landscape of the area is currently undergoing environmental changes (e.g. crop and land use conversion practices, soil degradation) and socio-economic ones (deagrarianization, farmers' suicides (Muenster 2012)), driven by agricultural intensification. These changes result in a transformation of landscapes (land use conversion) and livelihoods (deagrarianization) which particularly affect small agricultural communities and those whose livelihood strategies were based on rice cultivation in the past. In this research, we aimed to explore local people's ecological and agricultural knowledge, as well as the social transformation processes taking place in agrarian communities in Wayanad.

The social-ecological study is one outcome of the BioDIVA research project (www.biodiva.uni-hannover.de), an interdisciplinary research programme that brings together experts from varied disciplines such as rural sociology, ecology, spatial science, gender studies, and institutional and resource economics. Moreover, BioDIVA adopts a transdisciplinary approach that integrates non-academic knowledge in order to foster an understanding of real-world problems, such as changing agricultural practices in Kerala. The overall project aim is to develop strategies for the generation of transformation knowledge for sustainable agricultural futures in Wayanad. Transformation knowledge is the knowledge needed for a society to move towards to a more sustainable status while taking account of existing technical, social, legal, cultural, institutional and other conditions (Pohl & Hirsch Hadorn 2008; Cronin 2008).

Wayanad: a biocultural diversity hotspot

This social-ecological baseline study was conducted in Wayanad, a mountain plateau district of Kerala state located in the Western Ghats in South India. The Western Ghats are a bio-cultural diversity hotspot (Pretty et al. 2009; Brosius & Hitchner 2010) which has recently become one of the UNESCO Natural World Heritage sites (UNESCO World Heritage Centre 1992-2013 2012). Wayanad is notable for its large indigenous population, known as Adivasi, an umbrella term for indigenous or tribal population groups in India (Rath 2006). Wayanad has the highest proportion of Adivasi inhabitants in Kerala but also the highest level of poverty amongst Adivasis (Chathukulam & John 2006). The Kerala Government records distinguish between twenty Adivasi groups in Wayanad. They can be broadly classified into farming communities, landless agricultural labourers, artisan communities and hunter-gatherer communities (Nair 1911; Indian Institute of Management 2006). Many Adivasi communities have traditionally been involved in agriculture and paddy cultivation in particular.

However, socio-economic trends such as the growing tourism and real estate industries and ecological changes including irregular rainfall patterns are all modifying agricultural systems and affecting small-scale farming communities (Kumar 2005; Guillerme et al. 2011). Changing family structures and the reorganization of labour are further drivers of changes in the social organisation of Adivasi communities (Kunze & Momsen 2015). Overall, external challenges, such as the agricultural crisis in India (Lerche 2011) and land-use change, limit the options for Adivasi livelihood strategies in Wayanad (Kurup 2010; Kulirani 2011).

In the first part of this report we outline the design of the interdisciplinary study and discuss research objectives, research ethics, data collection methods, and data analysis. This section concludes with the presentation of the social-ecological web. The second part of the report focuses on the results of the social-ecological study and evaluates the social-ecological web as an interdisciplinary research tool, in the context of the challenges of integrating different disciplines and stakeholders in the research process. We argue that the social-ecological web is a hybrid between social and ecological networks, which serves both as a bridging concept and as a tool for depiction and analysis of the qualitative social-ecological data.

RESEARCH DESIGN

Transdisciplinary research consists of three phases: problem identification and structuring, problem analysis, and the practical application of results (Pohl & Hirsch Hadorn 2008). In addition, Novy et al. (2008) highlight three defining characteristics of transdisciplinary research: interdisciplinarity, problem-orientation and an equal relationship between researchers and project partners.

The present study was planned and implemented by the research team consisting of rural sociologists and ecologists. Each discipline was represented by two researchers, one German and one Indian, and an Indian research assistant. We built upon Pohl & Hirsch Hadorn (2008) notion of interdisciplinary research as a form of coordinated and integration-oriented collaboration between researchers from different disciplines. The research questions were formulated by researchers from the two disciplines, including the research assistants, who formulated research questions from their own disciplinary perspective. Two main research interests were at the centre of this inquiry: first, ecological knowledge and agricultural practices and second, the multiple meanings of social-ecological transformation processes in Wayanad district in Kerala.

The comparative social-ecological study investigated communities of two landowning Adivasi groups, the Kuruma and Kurichya, and one landless group, the Paniya. By comparing three contrasting Adivasi communities, we hoped to shed light on the nature and causes of the social-ecological changes occurring amongst rural communities in Wayanad.

Doing inter-and transdisciplinary research requires a sound research design, which needs to be developed jointly by all researchers involved in the study right from the start. Our research design included the definition of common research ethics, an interdisciplinary list of research questions and objectives, the joint field site selection and procedures for data collection and analysis.

Research ethics

The research ethics were embodied in a participation agreement between the researchers and the respondents and an information sheet for the participants who agreed to participate in the study. Both documents were written in English and the local language Malayalam in order to make sure that the respondents understood the overall objective of the study. Once the communities had been selected, we approached the head of each Adivasi community to ask for official permission to undertake the research and handed out the information sheet and a copy of the participation agreement.

Data collection methods

This qualitative study was carried out in March till May 2011 in three Adivasi villages: Kalluvayal (Kuruma), Maanikazhani (Kurichya), and Thannikunnu (Paniya), all located in Wayanad district. Random sampling was used for the selection of the villages; the choice of participants was based on snowball sampling (Newing et al. 2011). Three methodological tools were used for triangulation. First, we conducted semi-structured key informant interviews with the community chief of each settlement on 1) ecological knowledge and management practices and 2) social-ecological transformation processes. Second, we asked women and men separately to prepare village maps and seasonal calendars (participatory methods). This division appeared fruitful to gain gendered perspectives on the agricultural practices and village structures. Third, we carried out three focus group discussions with (ideally) five women and five men from each community.

The process of data collection was shaped by feedback loops between Indian and German researchers and between researchers and the Indian assistants. Reflexivity on methodology is crucial for interdisciplinary research processes (Jackson 2006; Padmanabhan 2011). The constant academic exchange between the Indian and German researchers including Indian research assistants enabled us to critically reflect upon the whole study process and especially on the design of the research questions. Based on the assistants' feedback on the interview dynamics observed in the field, the researchers reformulated and restructured the questions accordingly, which improved the effectiveness of the interviews in the field.

Data analysis: the social ecological web

Integration is a fundamental requirement for interdisciplinary research (Bergmann et al. 2010). The combination of knowledge from various disciplines requires the creation of methods for integration and communication to overcome terminological differences. We developed the social-ecological web as a bridging concept that seeks to integrate knowledge from rural sociology and ecology. A bridging concept is a common conceptual framework that facilitates analysis. Deppisch & Hasibovic (2011) note the importance of appropriate timing in the development of a bridging concept: the decision on whether to introduce it at the very beginning or to develop it jointly in the course of the interdisciplinary process. In this study, the social-ecological web was developed during the process of analysis.

The social-ecological web is analogous to the food webs used in ecology to analyse trophic interactions, i.e. food relations. The basic idea of food webs is to map relationships between different species that inhabit a specific ecosystem on the one hand and to reveal the organization of this community on the other. Food webs vary in complexity, focus and scope depending on the studied system and the pursued goal (Sunderland et al. 2007). Just as organisms interact with each other in an ecosystem, different components in an agrarian system are linked in a similar way. Therefore, we applied the ecological method of food webs to analyse the qualitative data; replacing organisms by social and environmental topics (e.g. livelihood strategies, natural resources, and paddy cultivation). The initial idea was to map the complexities of the social-ecological system and to identify links between different components.

How to construct a social-ecological web

The construction of a social-ecological web is carried out in four steps. First, the components that describe the observed system are identified. All four researchers analysed the qualitative interview data and visual material collected through participatory method, from both disciplinary viewpoints, to identify key categories relevant to the initial research questions and interests. Then, each group of researchers discussed the results and their importance for an understanding the multiple meanings of social-ecological change in Wayanad. The aim was to determine key components of the social-ecological system (dots in Fig. 1-3). Second, we synthesised the disciplinary outcomes and pooled components for simplification (e.g. livelihood strategies as a composite of formal occupation, women's education and their empowerment). Third, we identified links between the components based on different analytical procedures (lines in Fig. 1-3). We identified direct relationships (component A affects component B or vice versa) based on the interview data. This enabled us to grasp the actors' perspectives of the system's complexity. Indirect relationships (component C influences component A through component B) were determined from the researchers' disciplinary perspectives. Fourth, we indicated the direction of action for these relationships by arrow heads. Direct and indirect interrelations and the direction of action indicate on-going changes in the system.

RESULTS AND DISCUSSION

Comparing three Adivasi communities using the social-ecological web

In this section, we highlight some of the most pronounced observations and findings of our social-ecological study. The social-ecological webs (Fig. 2-4) reveal that the three Adivasi communities are structured differently and face dissimilar changes. The components of the social-ecological system (dots in Fig. 1-3) are of different importance for the Kuruma, Kurichya, and Paniya communities. Also the number of interrelations (lines in Fig. 1-3) between the components differs in each community. Taking the number of interrelations as an indicator of the magnitude of change, the Kuruma community (41 interrelations; Fig, 1) is undergoing most change, followed by the Paniya (39; Fig. 3) and lastly the Kurichya community (16; Fig. 2), which is experiencing the least change.

Unlike the Kuruma and Kurichya, the Paniya's livelihood strategies are strongly influenced by other web components such as deforestation, paddy cultivation, and environmental changes (Fig. 3). This leads to the conclusion that their livelihood strategies are currently changing most, compared to the other two communities. Based on our interpretation of the data, the forest has a stronger meaning for the Paniya than for the Kuruma and Kurichya. In the past, the Paniya lived in the forest (Nair 1911); as such deforestation has a huge impact on their relationship with nature and community life. In particular, members of the Paniya community referred to the negative effects of deforestation on the environment and on the use of natural resources and paddy cultivation. In line with Mohindra et al. (2010), we found that alcohol consumption is also a severe problem in the Paniya community. This became very clear during the interviews, which revealed the highly disruptive effect of alcohol consumption on family structure and the gendered division of roles and responsibilities.

Among the Kurichya and Kuruma, most of the landholders are agriculturalists, and agricultural practices such as paddy cultivation are at the centre of community life. But a closer look at the social-ecological web for the Kuruma community reveals that almost all components are interrelated (Fig. 1). Hence, it seems that the whole community structure is currently in a phase of reorganisation. Unlike the landless Paniya, who also find themselves in a stage of reorganisation, the landowning Kuruma have the power to partially control the changes taking place in their community. As landowners, they are in the position to take agricultural decisions in response to market demand. For example they increased vegetable cultivation some years ago as the market price of rice was no longer profitable (Kerala State Land Use Board 2006). Furthermore, the Kuruma do not depend on agricultural labour; therefore, they have the option to shape their livelihood strategies, for example by seeking higher education and formal employment. However this changes agrarian relations within the community due to reduced time available for agricultural work.

In contrast, social organisation in the Kurichya community, for example family structure and gender relations, appears to be largely unaffected by changes so far (Fig. 2). Indeed, compared with the other two, the Kurichiya community retains a more traditional social organisation. Of modern socio-economic institutions, only the market has some impact, on their agriculture; Kurichiya farmers now cultivate modern rice varieties on a small portion of their land for sale.

Despite these differences, there are also similarities between the three communities. Respondents all stated that on-going deforestation is the main driver of environmental degradation, e.g. changing rainfall patterns, which in turn has negative effects on agriculture, especially paddy cultivation. Furthermore, logging negatively affects the nutrition patterns of the all three communities. In the past, the forest was used as a resource for extraction of edible plants and hunting game (Münster & Vishnudas 2012). Today, this is hardly possible anymore due to habitat loss as well as a hunting ban decreed by the central government under the provisions of the Indian Wildlife Protection Act (Government of India 2012). The availability and/ or quality of natural resources (e.g. edible plants, fish) are important for the livelihood strategies of the Kuruma and Paniya communities due to the increasing cost of food purchased for consumption. Kurichya and Kuruma respondents considered intensified cultivation practices to be the cause of the declining quality and quantity of natural resources available.

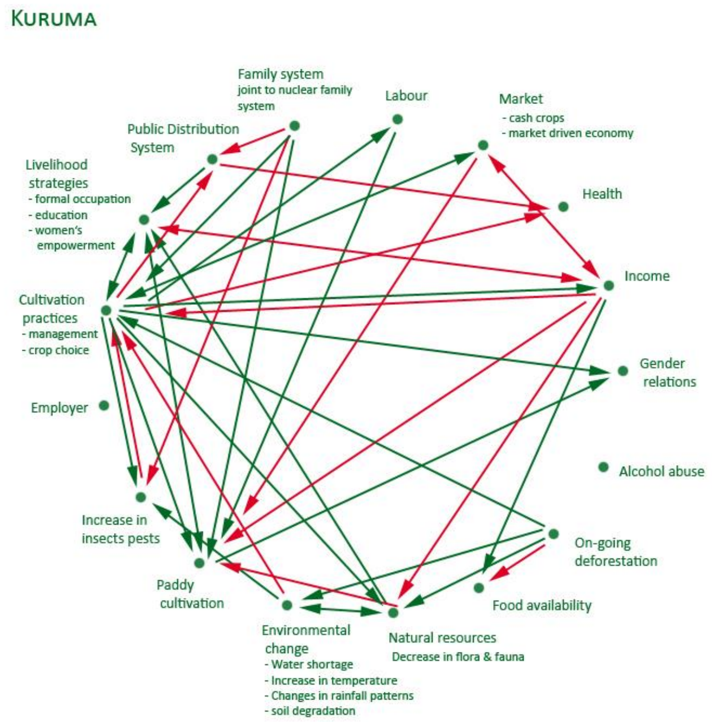

Figure 1: Social-ecological web of a Kuruma community. Dots: components important for the system derived from the data; green lines: direct interrelations between components, based on information given by participants; red lines: indirect interrelations, identified by data interpretation; arrows: direction of action, indicating on-going change processes.

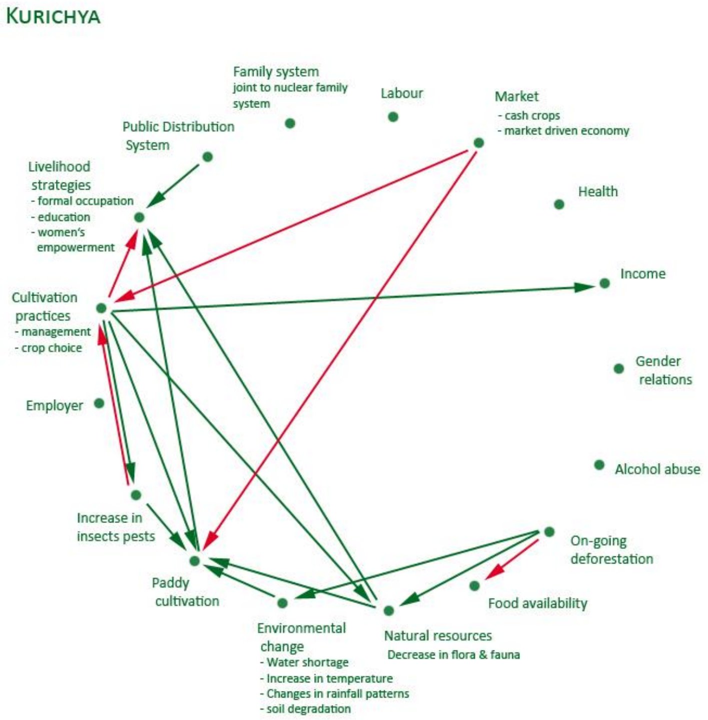

Figure 2: Social-ecological web of a Kurichya community. Dots: components important for the system derived from the data; green lines: direct interrelations between components, based on information given by participants; red lines: indirect interrelations, identified by data interpretation; arrows: direction of action, indicating on-going change processes.

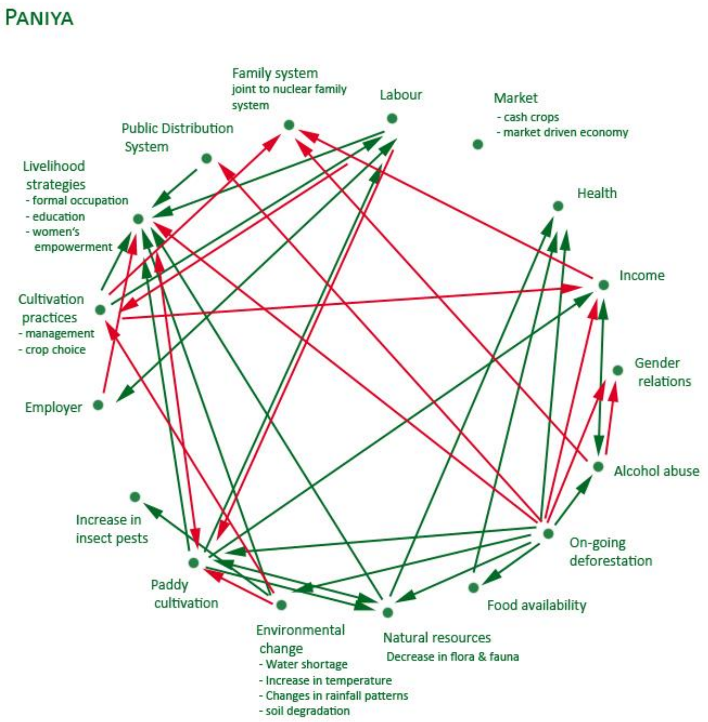

Figure 3: Social-ecological web of a Paniya community. Dots: components important for the system derived from the data; green lines: direct interrelations between components, based on information given by participants; red lines: indirect interrelations, identified by data interpretation; arrows: direction of action, indicating on-going change processes.

The Social-ecological web method – a useful tool?

The social-ecological web is the graphical depiction of the current state of a particular social-ecological system; in this case each of the three webs depicts an indigenous farming system in Wayanad. It is a useful tool that helps to simplify, portray and categorise the complexity and structure of an agricultural system, which leads to a better understanding of the system. It identifies important system components and those components most responsible for changes in the system. As such, the social-ecological web is a useful tool for a comparative analysis, as in our case, where it highlighted the differences between three Adivasi communities.

One limitation is that the web does not quantify the relative importance of the different components in the social-ecological system. Based on the available data this quantification was not possible. One option to improve the social-ecological web could be to ask the participants to rank the components according to their importance similarly as in Net-Map exercises (Schiffer & Hauck 2010; Schiffer 2007). Further enhancement of the social-ecological web method could be achieved by a participatory development of the webs. For example farmers could draw interrelations between components suggested by the researchers. Moreover participants could add components they think the researchers missed out. Using a participatory approach would also allow the formulation of social-ecological webs for the past and the future, which would highlight change processes even better. To complement this study, it would be interesting to use the same method with non-indigenous farmers in order to highlight the differences between different social classes and ethnic backgrounds, which are so important in such a culturally diverse country as India.

Although the idea of the social-ecological web was taken from food webs and thus ecology it became obvious during the critical reflection that this social-ecological web is similar to the methods used in social science e.g. Net-Maps or social network analysis (Schiffer 2007; Scott 2000). This leads to the conclusion that ecology and social science actually use similar methods. Therefore the social-ecological web is a kind of hybrid between methods from social and ecological science and thus an interdisciplinary tool that is easy to understand and use for both disciplines. It also fulfils the requirements of a bridging concept, by integrating knowledge from different disciplines and helping to overcome terminological differences.

The two objectives of this study were to learn about 1) the ecological knowledge and agricultural practices of the communities and 2) the social-ecological transformation processes taking place. It turns out to be difficult to tackle both issues at once. The social-ecological web method is an effective way to depict relationships between social and ecological components within an agrarian system and to analyse indicators of changes in agricultural practices. For detailed analysis of the ecological knowledge of members of the community, the social-ecological web is of limited use. The linkages between different ecological components, such as pest species, paddy cultivation or deforestation, as explained by farmers, offer some insight into their ecological knowledge. Nevertheless, interviews and ethno-ecological exercises might be a more appropriate methodological tool to elucidate farmers' ecological knowledge (Martin 2004).

Challenges of integrating different disciplines and stakeholders

After having explained and discussed the use of the social-ecological web for this interdisciplinary study, we now focus on the challenges of integrating more than one discipline into the design of a research project. We consider that communication between the two disciplinary teams, including the Indian assistants, was the key to overcoming disciplinary boundaries, by establishing feedback loops within the research process from the very beginning of the study. This is in line with transdisciplinary reflections on the research process that emphasise reflexivity and the importance of feedback loops (Novy et al. 2008). Discussions among the researchers led to a common understanding of the research questions and to the necessary reformulation of the research questions, from the initial academic jargon into a simplified language. Nevertheless, for the data collection we used only qualitative methods from social science; methods used in ecology are quite different so that it is difficult to combine the two. To analyse the data we developed the social-ecological web, a tool which turned out to be a hybrid between social network analysis and ecological food webs. This social-ecological web allows for the visual portrayal of the complexity of a social-ecological system and enables researcher from different disciplines to better understand the changes occurring in agrarian communities.

Furthermore the experience of carrying out this social-ecological study provided insights into how stakeholders can be integrated into the research process. The tandem approach, whereby each team was composed of a German and an Indian researcher, allowed for an informal access to the Adivasi communities; performing as an intercultural team helped to overcome language barriers and cultural biases. In addition, the dual role of our Indian tandem partners being both staff members of the M.S. Swaminathan Research Foundation (MSSRF) and BioDIVA´s project partners led to a greater acceptance of the social-ecological study due to MSSRF´s high reputation among the Adivasi farmers and within Wayanad as a whole.

CONCLUSION

In this paper, we have described how ecologists and rural sociologists integrated their research interests into an interdisciplinary social-ecological study. The overall objective of this baseline study was to better understand changes occurring in the social-ecological system in Wayanad, Kerala. Central to this study was joint data collection and the development of an interdisciplinary concept, the social-ecological web, designed as a bridging concept to facilitate the integration of knowledge from social and natural sciences.

The social-ecological web is a useful tool to illustrate and to compare the complexities of three different agrarian systems. The comparative approach reveals the differences among the Kuruma, Kurichya and Paniya groups, in terms of the structural changes that are occurring in the communities, the interrelations among system components, and the overall number of interrelations, which together describe the degree of change in the three social-ecological systems. The results of the comparative study between the three Adivasi groups show that the social-ecological system is modified by different components in each case. For example, deforestation negatively affects livelihood strategies of the Paniya. For the Kuruma and the Kurichya, market mechanisms influence the traditional agricultural system e.g. the choice over crops and cultivation practices. Common to all groups is deforestation as the major driver for environmental change, the loss of natural resources and consumption habits. Overall, we can conclude that changes in the agrarian system strongly shape social transformation processes in all three communities.

As a problem-oriented hybrid between social and ecological network analysis, the social-ecological web is a useful tool that facilitates interdisciplinary dialogue by visualising the dominant themes identified through data analysis. It could be further developed in a transdisciplinary manner by involving stakeholders.

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Summary

Around the globe, natural and agrarian landscapes are subject to agricultural intensification to meet the increasing and changing demands for resources of the growing population. This intensification takes place at two different scales: (1) At a landscape scale by reducing natural and semi-natural habitats to make room for the expansion of agriculture through monocultures and few crop types. (2) At a local scale, agricultural intensification implies shifts in agronomic practices such as the increasing application of agrochemicals, the use of heavy machinery, the cultivation of improved crop varieties and the reduction of genetic crop diversity. A decline of agrobiodiversity and associated ecosystem functions and services are one of the consequences, yet a changing agricultural system also impacts the social-ecological system. These transformations also affect small-scale and subsistence farming in the tropics. This thesis focuses on paddy cultivation systems in Wayanad district, Kerala State, South India and provides new results about effects of land-use change and agricultural intensification on agrobiodiversity and social-ecological processes.

In Wayanad, paddy cultivation has a very long tradition and is closely linked to the culture and religion of the inhabitants, especially in case of indigenous communities. However, traditional paddy cultivation is gradually intensified, mainly by the use of chemical fertilisers, insecticides and machinery as well as cultivation of high yielding varieties. Driven by the commercialisation of agriculture, paddy land has been and still is transformed to cultivate cash crops such as bananas, ginger, cassava or arecanut. Furthermore, increasing amount of semi-natural habitats such as homegarden polycultures is converted into simplified plantations.

For the ecological studies of the first and the second chapter of this thesis, we selected 18 paddy fields, which were cultivated by local farmers applying either high-intensity or low-intensity management. For the analysis, we focused on the three major agronomic practices, namely the amount of fertiliser application, insecticide application and weeding. Paddy fields were located either next to homegarden polycultures or banana monocultures. Samples were taken in three transects: (1) at the edge, close to adjacent habitat, (2) in the centre and (3) at the bund of the fields to consider possible edge effects. Additionally, we mapped the landscape components within a 500m radius around each field. The social-ecological study of the third chapter focuses on the three largest indigenous communities, the landowning agriculturalists Kuruma and Kurichya and the Paniya who are predominantly landless, agricultural labourer.

In the **first chapter** we analyse the response of paddy weeds, pests and predators to agricultural intensification at a local and landscape scale. Weeds, planthoppers and spiders were collected in the 18 paddy fields described above. The results showed that adjacent banana monocultures enhanced weed and planthopper population. Furthermore, the abundance of planthoppers was positively related to the density of weedy grasses but negatively affected by weed diversity (dominated by dicots). Spiders in contrast, benefited from weed diversity. However, spider population was mainly driven by prey availability. Increased fertiliser application had an indirect positive effect on spiders through increased prey abundance and weed richness. Spider abundance and richness decreased with increasing distance from the field edges, indicating influences of adjacent habitat on paddy field colonisation. The findings of this study suggest that paddy cultivation in Wayanad should consider the identity of adjacent habitat and weeds (monocots vs dicots) but also the amount of applied fertilisers to maintain a balanced agroecosystem.

The **second chapter** particularly focuses on the spider community in paddy fields. In addition to the abundance of the main spider families, we considered different web types as well as potential prey. Furthermore, effects of landscape characteristics and cultivation practices are taken into account. The analysis highlighted that the major determining factor for overall spider and web abundance was the prey availability; hence, the spider community in this paddy fields was driven by bottom up effects. A closer look at different families and web types revealed differences within this general pattern. For the web building Tetragnathidae and Linyphiidae Lepidoptera and leafhopper abundance were most important while Araneidae responded to Lepidoptera. The hunting spider Oxyopidae responded positively to Lepidoptera, leafhoppers and other insects. For this family we also found a slight negative effect of increasing herb cover in the paddy fields. The number of Salticidae and Lycosidae, also ahunting spiders, were only correlated with increasing numbers of Lepidoptera. Diverging results for web and spider abundances suggest that spider web sampling can be a useful complement to spider sampling. Furthermore, huge numbers of tetragnathid webs, which are easy to observe in the field, can be an indicator for the farmers to check their fields for possibly harmful infestation with rice pests.

In the **third chapter,** we focus on a social-ecological approach to assess the ecological knowledge and agricultural practices as well as the multiple meanings of social-ecological transformation processes. This qualitative study focused on the three major indigenous communities and their agrarian systems in Wayanad. We used three methodological tools, namely key informant interviews, village maps and seasonal calendars and focus group discussions. Central to this study was the development of a social-ecological web, which is understood as a bridging concept that integrates knowledge from social and natural science. This method is a useful tool to illustrate and compare the three different agrarian systems existing in Wayanad. Our results revealed that land-use change and intensification causes different degrees of social-ecological transformation among the three indigenous communities. Furthermore, the communities are affected by different factors of this change. For instance, the Kurichya's family structure remains largely unaffected so far while the Kuruma increasingly seek higher education and formal employment but deforestation negatively impacts livelihood strategies of the Paniya.

Overall, we argue that paddy agroecosystems in Wayanad were mainly driven by bottom-up effects: increasing resources led to an increase of individual numbers in higher trophic levels. Adjacent monocultures such as banana fields could enhance the population of rice weeds and pests. Intensification at the local scale had only minor effects, which may indicate that the intensification of paddy cultivation in Wayanad did not yet reached disastrous dimensions. Additionally, land-use change and agricultural intensification not only impact the ecological system, but also shape social-ecological transformation processes, which indicates the importance to examine such systems from an interdisciplinary angle.

Zusammenfassung

Weltweit sind natürliche und landwirtschaftliche Landschaften agrarischer Intensivierung ausgesetzt um den steigenden Resourcenbedarf der wachsenden Bevölkerung zu decken. Diese Intensivierung ist auf zwei Ebenen zu beobachten: (1) Auf Landschaftsebene durch die Beschneidung natürlicher und naturnaher Habitat um Platz für sich ausweitende Agrarflächen zu schaffen, durch das Anlegen von Monokulturen sowie durch einen Veränderte Auswahl der Feldfrüchte. (2) Auf lokaler Ebene beinhaltet landwirtschaftliche Intensivierung die Veränderung der Anbaumethoden wie beispielsweise der Erhöhte Einsatz von Agrarchemikalien, die Einführung schweren Geräts, der Anbau von Hochertragssorten sowie der Verlust genetischer Vielfalt. Der Rückgang von Agrarbiodiversität und den mit ihre verbundenen Ökosystemfunktionen und -dienstleistungen ist eine Konsequenz, aber ein verändertes landwirtschaftliches System beeinflusst auch das sozial-ökologische System. Diese Transformationen wirken sich auch auf Kleinbauern und Eigenbedarfslandwirtschaft in den Tropen aus. Diese Dissertation befasst sich mit dem Reisanbau in Wayanad, Kerala, Südindien und liefert neue Ergebnisse zu Auswirkungen von Landnutzungswandel und landwirtschaftlicher Intensivierung auf Agrarbiodiversität und sozial-ökologische Prozesse.

Reisanbau hat in Wayanad eine sehr lange Tradition und ist stark mit Kultur und Religion der Bevölkerung verbunden, vor allem im Falle der indigenen Bevölkerungsgruppen. Allerdings wurde bzw. wird der traditionelle Reisanbau graduell intensiviert, hauptsächlich durch die Einführung chemischer Düngemittel und Insektizide, Landmaschinen und Hochertragsorten. Aufgrund der Kommerzialisierung der Landwirtschaft wird Reisland umgewandelt um cash crops wie beispielsweise Bananen, Ingwer, Cassava oder Arekaplamen anzubauen. Desweiteren werden immer mehr Flächen naturnaher Habitate wie strukturreiche Hausgärten zu vereinfachten Plantagen modifiziert.

Für die ökologischen Studien des ersten und zweiten Kapitels der Dissertation wurden 18 Reisfelder ausgewählt. Die Bauern bewirtschafteten diese entweder intensiv oder wenig intensiviert. In die Analyse flossen die drei wichtigsten Bewirtschaftungsmaßnahmen ein, nämlich: die Menge der ausgebrachten Düngemittel, Verwendung von Insektiziden und Jäten. Die Reisfelder grenzten entweder an Hausgärten oder Bananen Monokulturen. Proben wurden in drei Transekten gesammelt: (1) am Rand der Feldes, nahe des angrenzenden Habitats, (2) in der Mitte des Feldes und (3) auf dem Damm des Feldes, um mögliche Randeffekte berücksichtigen zu können. Darüber hinaus wurden due Landschaftkomponenten innerhalb einen 500m Radius um jedes Feld kartiert. Die sozial-ökologische Studie des dritten Kapitels fokussierte sich auf die drei größten indigenen Gruppen in Wayanad, die landbesitzenden Landwirte Kuruma und Kurichya, sowie Paniya, die hauptsächlich landwirtschaftliche Arbeiter ohne eigenen Landbesitz sind.

Im **ersten Kapitel** analysieren wir die Reaktion von Unkräutern, Schädlingen und Prädatoren auf landwirtschaftliche Intensivierung auf lokaler und Landschaftebene. Unkräuter, Zikaden und Spinnen wurden in den 18 oben beschriebenen Feldern gesammelt. Die Ergebnisse zeigten, dass angrenzende Bananen Monokulturen Unkräuter und Zikaden fördern. Weiterhin war die Zikadenabundanz positive von der Dichte von Grasunkräutern beeinflusst, jedoch negativ von der Unkrautdiversität. Die Spinnen hingegen profitierten von der Unkrautdiversität. Jedoch war die Spinnenpopulation hauptsächlich durch die Beuteverfügbarkeit bestimmt. Erhöhter Eintrag von Dünger hatte einen indirekten positiven Einfluss durch erhöhte Beuteabundanz und Unkrautdiversität auf Spinnen. Spinnendiversität und -abundanz nahm mit größerer Entfernung von Feldrand ab, was darauf hin deutet, dass die Besiedlung des Feldes vom angrenzenden Habitat beeinflusst ist. Die Resultate dieser Studie zeigen darauf hin, dass der Reisanbau in Wayanad die Identität des angrenzenden Habitats sowie die der Unkräuter (Monokotyle vs. Dikotyle) berücksichtigen sollte, aber auch die Menge eingebrachten Düngers, um ein ausgeglichenes Agrarsystem zu erhalten.

Das **zweite Kapitel** richtet sein Augenmerk auf die Spinnengemeinschaft der Reisfelder. Neben Spinnenfamilien betrachten wir verschiedene Spinnennetztypen sowie potenzielle Beute. Weiterhin werden Landschaftscharakteristiken und Anbaupraktiken berücksichtigt. Die Auswertung zeigte, dass der hauptsächlich bestimmende Faktor der angesamten Spinnen- und Netzabundanz die Beuteverfügbarkeit ist. Folglich wird die Spinnengemeinschaft in den betrachteten Reisfeldern von bottom-up Effekten bestimmt. Ein näherer Blick auf die verschiedenen Familien und Netztypen zeigte Unterschiede innerhalb des allgemeinen Musters. Für die netzbauenden Tetragnathidae and Linyphiidae waren Lepidoptera und Zikaden (beides potenzielle Schädlinge) am wichtigsten, während Araneidae positiv mit Lepidoptera korreliert waren. Die frei jagenden Oxyopidae reagierten positiv auf Lepidoptera, Zikaden und andere Insekten. Für diese Familie wurde zudem ein leicht negativer Effekt von zunehmender Pflanzendeckung gefunden. Die Zahl der Salticidea und Lycosidae nahm mit höherer Lepidoptera Zahl zu. Divergierende Ergebnisse für Spinnen- und Netzabundanzen deutet daruaf hin, dass die Spinnennetzeaufnahme eine sinnvolle Ergänzung zur Aufnahme von Spinnen darstellt. Des Weiteren können hohe Zahlen von Tetragnathidae Netzen, die im Feld einfach zu beobachten sind, den Bauern als Indikatoren für einen eventuell kritischen Schädlingsbefall des Reises dienen.

Im **dritten Kapitel** konzentrieren wir uns auf einen sozial-ökologischen Ansatz um das ökologische Wissen, landwirtschaftliche Praktiken sowie die multiple Bedeutung sozial-ökologischer Transformationsprozesse zu untersuchen. Für diese qualitative Studie fokussierten wir uns auf die drei größten indigenen Bevölkerungsgruppen und ihre Landwirtschaftsysteme in Wayanad. Wir verwendeten drei methodische Werkzeuge, nämlich key informant Interviews, villige maps and seasonsal calendar, and Fokusgruppendiskussionen. Zentral für diese Studie war die Entwicklung des sozial-ökologischen Netzes, welches ein Brückenkonzept darstellt, das Erkenntnisse aus Sozial- und Naturwissenschaften integriert. Diese Methode ist ein nützliches Werkzeug um die verschiedenen Agrarsysteme in Wayanad zu illustrieren und zu vergleichen. Unsere Ergebnisse zeigten, dass Landnutzungswandel und Intensivierung ein unterschiedliches Ausmaß sozial-ökologischen Wandels unter den drei indigenen Gruppen verursachen. Weiterhin werden die Gruppen von verschiedenen Faktoren beeinflusst. Beispielsweise ist die Familienstruktur der Kurichya bislang weitestgehend unbeeinflusst, während die Kuruma zunehmend nach höherer Bildung und formalen Beschäftigungen streben und die Existenzgrundlage der Paniya negativ von Abholzung betroffen sind.

Zusammenfassend argumentieren, dass die Agrarbiodiversität in Reisanbausystemen in Wayanad hauptsächlich durch bottom-up Effekte bestimmt waren: erhöhte Resourcenverfügbarkeit führte zu höheren Individuenzahlen in höheren trophischen Ebenen. Überdies förderten Monokulturen wie beispielsweise Bananenfelder, die Populationen von Reisschädlingen und Unkräutern. Intensivierung auf lokaler Ebene hatten nur einen geringen Effekt, was möglicherweise daraufhin deutet, dass die Intensivierung des Reisanbaus in Wayanad noch keine desaströsen Ausmaße erreicht hat. Weiterhin beeinflusst Landnutzungswandel und landwirtschaftliche Intensivierung nicht nur das ökologische System sondern bestimmt auch sozial-ökologische Transformationsprozesse, was auf die Wichtigkeit hinweist, ein System aus einem interdisziplinären Blickwinkeln zu betrachten.

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CONFERENCE CONTRIBUTIONS

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Gastdozentur im Rahmen der Lehrveranstaltung Soziale Ökologie - Konzeptionelle und methodische Grundlagen und ausgewählte Forschungsfelder von Prof. Dr. Sabine Hofmeister. Thema "Agrarbiodiversität und Gender". 6 January 2015, Universität Lüneburg, Germany.

SCB Asia 2014, The 3rd Asia Regional Conference of the Society for Conservation Biology - Asia Section. Poster presented on "Paddy intensification and landscape context effects spider, leafhopper, and plant communities in southern India". 19-22 August 2014, Melaka, Peninsular Malaysia.

Challenges of Urban and Rural Transformation, 20th International Symposium on Society and Resource Management. Presentation on "What is sustainable use of agrobiodiversity? Integrating perspectives on land use change and social transition". 09-13 June 2014, Hannover, Germany.

Tropical organisms and ecosystems in a changing world. Annual Conference of the Society for Tropical Ecology. Presentation on "Spider-Cicada-Plant relationship in paddy fields of changing Indian landscape". 02-05 April 2013, Vienna, Austria.

SCB Asia 2012: Science, Policy, and Governance. The 2nd Asia Regional Conference of the Society for Conservation Biology – Asia Section. Poster presented on "Agricultural transformation in Wayanad: How does it affect spider diversity?". 07-10 August 2012, Bangalore, India.

Statusseminar der Sozial-Ökologischen Junior Forscher Gruppen. Presentation on "Sind Adivasi Bevölkerungsgruppen resilient gegenüber Transformationsprozessen? Eine sozial-ökologische Studie zu Wayanad, Südindien". 16-17 April 2012, Berlin, Germany.

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January 2009	Diploma in biology (Dipl. Biol.) at University of Göttingen, Germany
2008 – 2009	Diploma thesis *"Diversity of small mammals along a land-use gradient in Sulawesi, Indonesia"* at the University of Göttingen four month fieldwork in Sulawesi, Indonesia
2005 – 2008	Main studies Biology at University of Göttingen, Germany Major subject: Zoology Minor subjects: Botany and Geography
2003 – 2005	Basic studies in Biology at University of Göttingen, Germany Intermediate diploma in Zoology, Botany, Physics and Inorganic Chemistry
June 2003	Completion of secondary school (Abitur) in Biology, History and Geography at Albert-Schweizer-Schule Hofgeismar, Germany

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2009 – 2010	Research assistant in the AnimalBase Project Group, 2005-2009. AnimalBase. Early zoological literature online. - World wide web electronic publication (www.animalbase.uni-goettingen.de), University of Göttingen
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