UNIVERSITÄT BAYREUTH

Plant communities in field margins of agricultural landscapes: species distributions, functional traits, and contributions to landscape function

Dissertation

to attain the academic degree of Doctor of Natural Science (Dr. rer. nat)

of the Bayreuth Graduate School for Mathematical and Natural Sciences (BayNAT)

of the University of Bayreuth

Presented by

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Born on 03 February 1982 in Ismailia, Egypt

Bayreuth, March 2015

This doctoral thesis was prepared at the Junior Professorship of Biogeographical Modelling, University of Bayreuth between December 2011 and March 2015. It was supervised by Prof. Dr. Björn Reineking.

This is a full reprint of the dissertation submitted to obtain the academic degree of Doctor of Natural Sciences (Dr. rer. nat.) and approved by the Bayreuth Graduate School of Mathematical and Natural Sciences (BayNAT) of the University of Bayreuth.

Date of submission:	31.03.2015
Date of defense (disputation):	22.09.2015

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Dedication

To my late father “Elsayed Ali”.

His words of inspiration and encouragement

in pursuit of excellence, still linger on.

Summary

Most of the agricultural landscapes are a mosaic of cultivated fields, semi-natural habitats, human infrastructures and occasional natural habitats. Within such landscapes, linear semi-natural habitats often define the edges of agricultural fields, called “field margins”. Field margins are an important component of the agricultural landscapes as they are contributing positively to ecosystem functions by supporting biodiversity, preventing soil erosion, contributing in nutrient cycling and improving soil stability.

This thesis is aiming to further our understanding of the processes governing plant community structure and resulting functioning in agricultural field margins by focusing on describing naturally occurring plant communities of the field margins in the agricultural landscape of Haean-myun catchment in South Korea and how it can affect the ecosystem functioning (e.g. soil stability, soil erosion control), which consequently will help us to understand the functional role of the field margins as an important component of the agro-ecosystem. Our first study investigates how the local-scale management and the landscape-scale land-use influence the composition of plant communities of agricultural field margins, to understand how to improve the diversity of the field margins in agricultural landscapes. In the second study, we aimed to integrate vegetation characteristics and plant functional traits (PFTs) into a statistical model of abiotic soil characteristic effects on soil stability, towards an improved understanding of ecosystem functioning in agricultural landscapes. Finally, in the third study, we investigated how field margins in the agriculture landscapes can limit the soil erosion during the monsoon season, which will help us to better understand the function of an important ecosystem component like field margins within the agriculture landscapes, via testing the effect of its different management schemes at different slope degrees on sediment trapping.

To test how the local management “managed and unmanaged” and the landscape-scale land-use “percentage of non-farmed habitat” influence plant communities of agricultural field margins, we studied multi-facet plant community structure which includes alpha, beta and gamma diversities and species level characteristics such as rareness, growth forms, and dispersal types in hundred field margins in Haean-myun catchment, South Korea. We found that abandonment of local management in field margins positively influenced alpha diversity and especially the abundance of species that are rare and/or are characterized by abiotic dispersal and perennial growth forms. In contrast, local management of field margins resulted in lower alpha diversity and contributed to high beta diversity. The availability of landscape-scale non-farmed habitats influenced especially the diversity of managed field margins by increasing alpha diversity especially when focusing on more frequent species. The positive effect was highest for annual species independent of their dispersal mode.

For our second study, we used path model analysis to quantify the effect of plant functional traits (PFTs), abiotic soil characteristics (soil texture) and vegetation characteristics (vegetation cover and species richness) on three soil stability measures (soil aggregate stability, soil penetration resistance and soil shear vane strength) in 30 field margins in Haean-myun catchment, South Korea, in these models we studied also the importance of intraspecific trait variability (ITV) by comparing models that account or ignore for ITV. We found that, variance in soil stability was explained to varying degrees (from 81% for soil aggregate stability to 35% for soil shear vane strength). The three soil stability measures were mainly affected directly by root density, while PFTs and soil texture exerted indirect effects through root density and vegetation parameters, respectively. Including ITV improved model explained variance and goodness-of-fit in all cases.

In the third study on the effect of field margin's management and slope degree on sediment trapping, prior to the beginning of monsoon season, a total of 12 sites within Haean-myun catchment, South Korea, were equipped with Astroturf mats (n = 15 / site) which were placed before, within and after four different types of field margins: "managed flat", "managed steep", "natural flat" and "natural steep. Sediment was collected from the 12 sites after each rain event continuously until the end of the monsoon season. Using the linear mixed effect model allowed us to test the effect of management and slope degree on sediment trapping for the sediment collected within the field margin and the sediment difference between these collected after and before the four field margins' types. We found that in all cases, there is a positive relation between rainfall and sediment collected. Natural field margins showed high efficiency in reducing soil erosion in comparison to the managed ones. For the field margin slope, it showed effectiveness in combination with vegetation cover, as natural margins that have steep slopes had more sediment trapped in comparison to the managed margins. These findings allowed us to develop a functional framework of placement and designing of field margins within agriculture landscape to reduce soil erosion.

In this thesis, we developed several recommendations for improving the ecosystem functions in agricultural landscapes using the field margins as a functional component of the agroecosystem. We showed how important the local-management of the field margins and the surrounding landscape-scale land-use in maintaining the diversity in the agricultural landscapes. For areas like South Korea, new laws and strategies should be developed to control the field margin's local management, which will help in conserving the biodiversity by providing the suitable habitats for flora and fauna and consequently, will affect the soil quality and stability which will help in controlling the soil erosion happens during the monsoon time in South Korea. Furthermore, we demonstrated how essential is the field margin's plant functional community composition on soil stability as an important ecosystem function in the agricultural landscapes. Finally, we modified a pre-existing future decision support system (DSS) framework for the effective design and placement of the vegetated field margins within the agricultural field system to help in protecting soil erosion via field margins in agricultural landscapes that face monsoonal climate.

Zusammenfassung

Die Mehrheit der Agrarlandschaften bestehen aus einem Mosaik von bewirtschafteten Feldern, semi-natürlichen Habitaten, künstliche Infrastrukturen und zeitweise natürlichen Habitaten. Innerhalb dieser Landschaften werden Feldränder oft als lineare semi-natürliche Habitate charkterisiert. Die Feldränder stellen eine wichtige Komponente der Agrarlandschaften dar, da sie wichtige Ökosystemfunktionen wie z.B. die Förderung der Biodiversität und der Nährstoffkreisläufe, den Schutz vor Bodenerosion sowie die Erhöhung der Bodenstabilität übernehmen.

Die vorliegende Arbeit verfolgt das Ziel, ein besseres Verständnis über die Prozesse der Struktur der vorherrschenden Pflanzengemeinschaften und der daraus resultierenden Funktion der Feldränder zu erlangen, indem die natürlich vorkommenden Pflanzengemeinschaften der Feldränder in der Agrarlandschaft des Haean-myun Einzugsgebiets in Südkorea beschrieben werden. Desweiteren soll untersucht werden, in welchem Maße die Feldränder die Ökosystemfunktionen beeinflussen (z.B. Bodenstabilität, Bodenerosionskontrolle). Dies soll zu einem tieferem Verständnis der funktionalen Rolle der Feldränder als wichtige Komponente der Agrarökosysteme führen. Die erste Studie der vorliegenden Arbeit untersucht, wie sich das Management auf lokaler Ebene und die Landnutzung auf Landschaftebene auf die Komposition der Pflanzengemeinschaften der Feldrändern auswirkt, um ein besseres Verständnis darüber zu erlangen, wie die Diversität der Feldränder in Agrarlandschaften erhöht werden kann. Die zweite Studie dieser Arbeit zielt darauf ab, Vegetationscharakteristika und funktionale Pflanzeneigenschaften zusätzlich zu abiotischen Bodeneigenschaften in ein statistisches Modell der Bodenstabilität zu integrieren, um ein besseres Verständnis über die Ökosystemfunktionen in Agrarlandschaften zu erlangen. In dritten und letzten Teil der vorliegenden Arbeit wird untersucht, in welchem Ausmaß die Feldränder die Bodenerosion in Agrarlandschaften während der Mosunzeit vermindern. Dies soll zu einem verbesserten Verständnis über die Rolle der Feldränder als wichtige Komponente des Ökosystems innerhalb der Agrarlandschaften führen. In dieser Studie wird der Effekt verschiedener Management-Systeme und unterschiedlichen Hangneigungen auf den Sedimentrückhalt untersucht.

Um zu testen, wie sich das lokale Management “bewirtschaftet und nicht-bewirtschaftet“ und die Landnutzung auf Landschaftsebene im Sinne des Prozentanteils des nicht-bewirtschafteten Habitats auf die Pflanzengemeinschaften in den Feldrändern auswirkt, wurde die facettenreiche Struktur der Pflanzengemeinschaft in Hinblick auf die Alpha-, Beta-, und Gamma-Diversität und der Artniveau-Charakteristik wie Seltenheit, Wuchsform und Dispersionstypen in hundert Feldrändern im Haean-myun Einzugsgebiet untersucht. Die Studie ergab, dass der Verzicht auf lokales Management in Feldrändern die Alpha-Diversität und insbesondere das Artenreichtum der seltenen Arten und/oder die abiotische Verbreitung und perennierende Wuchsformen positiv beeinflussten. Im Gegensatz dazu führte ein lokales Management

der Feldränder zu einer niedrigeren Alpha-Diversität und einer höheren Beta-Diversität. Die Verfügbarkeit von nicht-bewirtschafteten Habitaten auf Landschaftsebene beeinflusste die Diversität der gemanagten Feldränder, insbesondere die Alpha-Diversität mit Fokus auf die häufiger vorkommenden Arten. Der stärkste positive Effekt auf die Alpha-Diversität wurde bei den einjährigen Arten unabhängig von deren Dispersionsgrad gefunden.

In der zweiten Studie nutzten wir die Pfad-Modell-Analyse um den Effekt der funktionalen Pflanzenmerkmale (PTFs), der abiotischen Bodeneigenschaften (Bodentextur) und der Vegetationseigenschaften (Grad der Vegetationsbedeckung und Artenreichtum) auf drei Bodenstabilitätskriterien (Bodenaggregatstabilität, Bodeneindringwiderstand und Bodenscherfestigkeit) in 30 Feldrändern im Haean-Einzugsgebiet in Südkorea zu untersuchen. Außerdem untersuchten wir die Bedeutung der intraspezifischen Merkmalsvariabilität (ITV) indem die Modelle, die ITV entweder berücksichtigten oder nicht berücksichtigten, verglichen wurden. Die Studie ergab, dass die Varianz der Bodenstabilität im unterschiedlichen Ausmaß erklärt wurde (zu 81% mit der Bodenaggregatstabilität und zu 35% mit der Bodenscherfestigkeit). Die drei Bodenstabilitätskriterien wurden hauptsächlich direkt durch die Wurzeldichte beeinflusst, während hingegen die PTFs durch die Wurzeldichte und die Bodentextur durch andere Vegetationsparameter eher indirekt beeinflusst wurden. Das Modell, welches die ITV berücksichtigte, erklärte die Varianz und die Anpassungsgüte in allen Fällen.

In der dritten Studie wurde der Effekt des Feldränder-Managements und der Hangneigung auf den Sedimentrückhalt untersucht, indem vor der Monsunzeit an 12 Standorten im Einzugsgebiet Haean Atroturf-Matten (n=15/Standort) installiert wurden und zwar vor, mittig und hinter vier verschiedenen Feldrand-Typen (bewirtschaftet+flach, bewirtschaftet+steil, nicht-bewirtschaftet+flach, nicht-bewirtschaftet+steil). Die Sedimentmenge wurde an den 12 Standorten nach jedem Regenereignis durchgehend bis zum Ende der Monsunzeit bestimmt. Mithilfe des linearen Mixed-Effect-Modells wurde getestet, in welchem Ausmaß sich das Management der Feldränder und dessen Hangneigung auf den Sedimentrückhalt auswirkt und wie sich die Sedimentmenge vor und hinter den vier Feldrandtypen unterscheidet. Die Studie ergab eine positive Korrelation zwischen Niederschlagsmenge und Sedimentmenge in allen untersuchten Fällen. Im Vergleich zu den bewirtschafteten Feldrändern zeigten die nicht-bewirtschafteten Feldränder eine erhöhte Effizienz bei der Verminderung der Bodenerosion. Im Falle der Hangneigung zeigte sich, dass auch hier die nicht-bewirtschafteten natürlichen Feldränder im Vergleich zu den bewirtschafteten Feldrändern in Kombination mit der Vegetationsbedeckung und bei starker Hangneigung am meisten Sediment zurückhielten. Die Ergebnisse erlaubten, ein Konzept zur Anordnung und Gestaltung von Feldrändern in Agrarlandschaften zur Reduktion der Bodenerosion zu entwickeln.

In der vorliegenden Arbeit haben wir mehrere Empfehlungen für eine Verbesserung der Ökosystemfunktionen in Agrarlandschaften in Bezug auf die Feldränder als funktionale Komponente des

Agrarökosystems entwickelt. Wir konnten zeigen, wie wichtig das lokale Management der Feldränder und die umgebene Landnutzung auf Landschaftsebene für den Erhalt der Diversität in Agrarlandschaften ist. Für Länder wie Südkorea sollten neue Gesetze und Strategien in Bezug auf die Kontrolle des lokalen Feldränderbewirtschaftung entwickelt werden, welche den Erhalt der Biodiversität durch die Bereitstellung von geeigneten Habitaten für Flora und Fauna unterstützen. Somit kann auch die Bodenqualität und Bodenstabilität beeinflusst und die Bodenerosion während der Monsunzeit in Südkorea kontrolliert werden. Darüber hinaus konnten wir zeigen, wie essentiell sich die Komposition der funktionellen Pflanzengemeinschaften der Feldränder auf die Bodenstabilität als wichtige Komponente der Ökosystemfunktion in Agrarlandschaften auswirkt. Schließlich konnten wir ein zuvor existierendes Entscheidungsunterstützungssystem modifizieren, welches eine effektivere Platzierung und ein effektiveres Design der Feldränder innerhalb der Agrarlandschaft erlaubt und als Bodenerosionsschutz insbesondere in vom Monsun beeinflussten Gebieten dient.

Acknowledgements

As the Messenger of Allah, **Muhammad (peace be upon him)** said: “the one who does not give thanks to people will not give thanks to Allah”, I’d like to take this opportunity to express my gratitude to the people who have been instrumental in the successful completion of this thesis. After **Allah (SWT)**, I would like to show my greatest appreciation to my doctor father “**Björn Reineking**”. I can’t say whether thanking him is enough for his tremendous support and help. I feel motivated and encouraged every time I discuss with him. Without his encouragement and guidance this project would not have materialized.

I am sincerely grateful to “**Tamara Münkemüller**” for her guidance, good ideas, useful critiques, and the uncountable helpful comments concerning our statistical analyses and also for her valuable help with writing and editing the individual manuscripts of this thesis.

As this thesis is part of the International Research Training Group ‘‘Complex TERRain and ECOlogical Heterogeneity” (TERRECO) (GRK 1565/1) funded by the German Research Foundation (DFG). I would like to thank the head of TERRECO, “**John Tenhunen**”, who gave me the opportunity to be part of this project, which gave my life a new and amazing direction.

I would also like to thank all my colleagues of the TERRECO project, who became close friends during the last years, especially “**Sebastian Arnhold**”, “**Eun-Young Jung**”, “**Marianne Ruidisch**” and “**Bumsuk Seo**” or “Alan” as he likes to be called, for their help and support during the field work in Korea, lab work in Germany and for their valuable comments. My special thanks go to “**Sina Berger**”, “**Kwanghun Choi**”, “**Kiyong Kim**”, “**Young-Sun Kim**”, “**Cosmas Lambini**”, “**Saem Lee**”, “**Mi-Hee Lee**”, “**Steve Lindner**”, “**Thinh Duy Nguyen**”, “**Hannes Oeverdieck**”, “**Silvia Parra**”, “**Jean-Lionel**”, “**Timothy Thrippleton**”, “**Chris Shope**” and “**Liesbeth van den Brink**” for the nice and crazy time that we spent together during the last years, especially in Korea.

I wish to give my great appreciation also to “**Sandra Thomas**”, “**Margarete Wartinger**” and “**Iris Schmiedinger**” for their outstanding help in the laboratory and office work.

Special thanks to special persons in my life, “**Yasser Awad**” who supported and encouraged me a lot during my first field work in Korea and during the semester he spent here in Germany. I will never forget his daily phone calls and the nice food that he kept sending it to me in Haean. “**Nedal Elshorbagy**” the person who always calling me wherever he is in this world, we may spent less than a year together in Germany, but he succeed in this short period to become so special to me. “**Ahmad El-Sherifi**” the one who I know since my childhood, even we didn’t meet since years, but he is always special.

Finally, no acknowledgments would be complete without giving thanks to my family. I am grateful to **my mum** for her patient encouragement and support throughout my whole life. She has instilled many admirable qualities in me and has given me a good foundation to meet life as it comes. Mum, you are a model of resilience, strength and character to me. Special thanks to my brother “**Deaa**” for his big support; I wish he will finish his master with dazzling brilliance. I should also thank my little monkeys; my niece “**Emily**” and my nephew “**Abdelrahman**”; just for calling me “Uncle Hamada”.

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List of abbreviations

CWM	Community weighted means
DSS	Decision support system framework
GLMM	Generalized linear mixed model
GoF	Goodness-of-fit
ITV	Intraspecific trait variability
LCBD	Local contributions to beta diversity
LME	Linear mixed effect models
MMF	Morgan-Morgan-Finney erosion model
MWD	Mean weight diameter
PFTs	Plant functional traits
PLS-PM	Partial least squares path modeling
RD	Root diameter
RDA	redundancy analysis
RDM	Root dry mass
REML	Restricted maximum likelihood
RHW	Root horizontal width
RL	Root length
RL	Root length
RSR	Root / shoot ratio
spc	Standardized path coefficients
SRL	Specific root length
TERRECO	Complex TERRain and ECOlogical Heterogeneity
WDPT	Water drop penetration time
α-diversity	Alpha diversity
β-diversity	Beta diversity
γ-diversity	Gamma diversity

Chapter 1: General introduction

1.1. Background and motivation

1.1.1 Field margins and their importance to agricultural landscapes

Agricultural landscapes cover approximately 50% of the earth's land surface, where one-third is planted with crops, while the other two-thirds dedicated to grazing land (Durán Zuazo & Rodríguez Pleguezuelo, 2008; USDA, 2013). One of the functional components of the agricultural landscapes is field margin, which is the vegetated strips of land lying between crop and field boundary, and extending to a limited distance into the crop (Greaves & Marshall, 1987; Hickey & Doran, 2004). Field margins are a key feature of agricultural landscapes, present in some forms at the edges of all agricultural fields (Marshall, 1988).

A series of extremely important roles for field margins have been identified, reflecting agricultural, environmental, conservational, recreational, and cultural or historical interests (Marshall, 1993; Marshall, 1995). New approaches to creating and managing field margins have shown the importance of these functions. Udo de Haes (1995) and de Snoo (1995) summarized four major concerns involved in field margin management as shown in Table 1.1. The effectiveness of field margins in contributing positively to landscape functions by reducing environmental impacts of human activities and providing the services (Table 1.1) depends on biological community composition, i.e., the establishment, presence and resilience of organisms occupying these niches. Although many researches on field margins have been conducted in Europe (Tarmi *et al.*, 2009; Ma *et al.*, 2013), a role of field margins in other ecosystems, like South Korean agricultural landscapes characterized by monsoon-rainfalls, is comparatively less studied.

In modern times, agriculture has seen major changes, with intensification of production, developments in machinery, crop protection and a need for larger field sizes. Land re-allotment programmes, in which ownership has been rationalized, have also been implemented in many countries. These developments have been accompanied by changes in field margins, often with the removal of features illustrated in Fig. 1.1.

Table 1.1. Major functions of field margins in agricultural landscapes.

Function	Role
Agronomy and animal husbandry	Define land ownership, provide stock fencing and shelter, provide windbreak for crops, enhance pollination, provide wood and wild game
Environmental	Control transport of pesticides, herbicides and nutrients; prevent erosion and siltation, influence snow and water distribution
Nature conservation	Provide species refugia, complement biodiversity by providing habitat, feeding and breeding locations, and movement corridors
Recreation and rural development	Provide field access, and areas for walking, driving, hunting; promote tourism via aesthetics, maintain culture and heritage

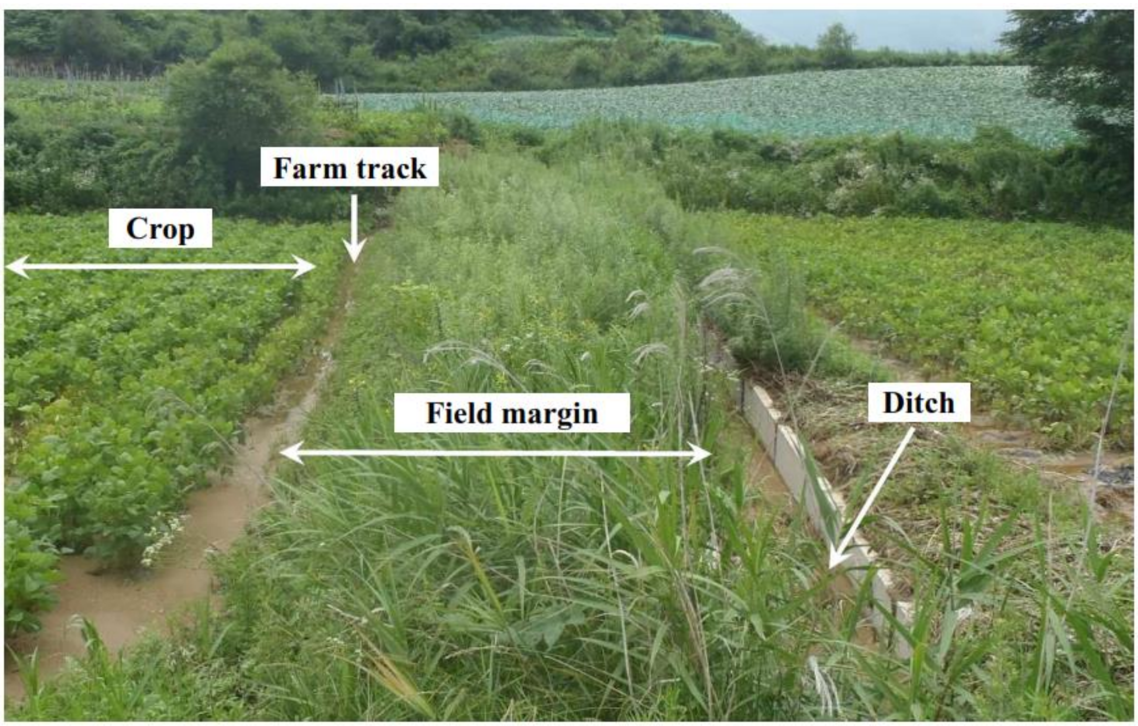

Fig. 1.1. Principal elements of a field margin in the agricultural landscapes (after Greaves and Marshall (1987)).

1.1.2 Diversity of the field margins

Field margin diversity is of great importance to the ecosystem in different ways: firstly, by increasing its productivity, as the more species found will lead to complementary patterns for using the ecosystem resources and also due to the mutual interactions between species (Tilman *et al.*, 1996; Loreau *et al.*, 2001; Hooper *et al.*, 2005; Cardinale *et al.*, 2006). Secondly, increasing the ecosystem stability, as larger number of species is essential to maintain the stability of ecosystem processes in changing environments (Chapin *et al.*, 2000). As from a functional point of view, species diversity is important as their individual traits and interactions contribute to maintain the functioning and stability of ecosystems and biogeochemical cycles (Lehman & Tilman, 2000; Naeem *et al.*, 2012). Thirdly, high diversity provides a buffer against environmental fluctuations, as the different responses of different species to these fluctuations will lead to more predictable ecosystem properties (Yachi & Loreau, 1999; Loreau *et al.*, 2001). Due to this relation between diversity and ecosystem functioning, problems will appear as a result of species losses, which is mainly due to human activities as it will consequently alter some of the key ecosystem processes, e.g. productivity and nutrient cycling, affecting the whole ecosystem services, which means, arguments for biodiversity conservation are mainly based on ecosystem services (Isbell *et al.*, 2011; Cardinale *et al.*, 2012).

One of the major threats to the biodiversity in the agriculture landscapes is the agriculture intensification which leads to a severe decline in the species diversity and as discussed earlier will affect the ecosystem functioning. Even with this agriculture intensification the field margins can play a conservation role, as it provides species refugia and complementing biodiversity by providing habitat, feeding and breeding locations (Ma *et al.*, 2013). So, in order to ensure an efficient conservation plane in agricultural landscapes, it is important to estimate the land-use and human impacts on biodiversity, especially on a landscape scale (Jost *et al.*, 2010; Hackman, 2015), species maintenance, functional and evolutionary processes at different spatial scales (Gering *et al.*, 2003; Brooks *et al.*, 2006; Lee & Jetz, 2008). To achieve this, all of the diversity components should be provided at the local (α-diversity), regional (γ-diversity) and among localities (β-diversity) scales (Buckley & Jetz, 2008; Jankowski *et al.*, 2009), which will help in conservation of biodiversity in order to reduce the unnaturally rapid extinction rates caused by human activities (Chapin *et al.*, 2000).

Currently, it became well known that the plant species growing in field margins are affected by the surrounding landscape via effects on the regional species pool and dispersal limitations (Pärtel *et al.*, 1996; Marshall *et al.*, 2006) and the management practices (Jobin *et al.*, 1997), so grasping how plant species growing in the field margins respond to different types of disturbances will help enriching their functions and roles within the agroecosystem.

1.1.3 Plant functional traits (PFTs) and ecosystem functioning

The high diversity of species makes a functional analysis of the importance of individual species challenging. The concept of plant functional traits (PFTs) promises to be a powerful approach in this context (Wellstein *et al.*, 2011). PFTs is a currently widely used expression in plant ecology (Díaz & Cabido, 2001; Hooper *et al.*, 2005; Lavorel *et al.*, 2007; Albert *et al.*, 2012), but its actual meaning still varies among authors. A plant functional trait is generally defined as any morphological, physiological or phenological feature measured at the individual level that impacts fitness (Violle *et al.*, 2007). It may be understood as a surrogate of a function (e.g. specific leaf area) or as this function itself (e.g. photosynthesis), with the difficulty to agree on the actual meaning of function (Calow, 1987; Jax, 2005). It is also considered as a trait that strongly influences organismal performance (McGill *et al.*, 2006) and/or individual fitness (Geber & Griffen, 2003; Reich *et al.*, 2003). Finally, it may be defined with respect to ecosystem functioning (McIntyre *et al.*, 1999) this is the case of functional effect traits, defined as those traits that have an impact on ecosystem functioning (Díaz & Cabido, 2001; Lavorel *et al.*, 2007). PFTs promise to allow for a process-based understanding plant community patterns at a manageable level of complexity. They provide a link between organism-centred and matter-flux-oriented perspectives on ecosystem ecology (Lavorel & Grigulis, 2012).

Understanding the processes that drive the degradation of ecosystem functions in agricultural landscapes is of pivotal interest given ongoing land-use and climate change (Cardinale *et al.*, 2012). Although ecosystem functions are strongly affected by the direct impact of abiotic drivers (e.g. soil moisture), it is also modulated by biotic factors (Loreau *et al.*, 2001). A number of studies has aimed at identifying the most important biotic drivers and it has been suggested that the functional composition of ecological communities is often more important for the maintenance of ecosystem functioning than species richness *per se* (Diaz *et al.*, 2006; Laughlin, 2014).

Different metrics of functional community composition can be measured in different ways. Recent studies suggest that community weighted means of functional traits (CWM), obtained by taking the mean trait value of a species weighted by its relative abundance in the focal community and then summed over all species (Garnier *et al.*, 2004). This relates better to ecosystem functioning than functional diversity metrics (Fortunel *et al.*, 2009; Laughlin, 2011). Even though CWM is commonly applied (Garnier *et al.*, 2004; Díaz *et al.*, 2007) this metric has the problem that it ignores intraspecific trait variability. However, intraspecific variability can be large and is often not random but a result of adaptation or phenotypic plasticity of traits either along environmental gradients (Sandquist & Ehleringer, 1997) or a response to biotic interactions (Gross *et al.*, 2009; Albert *et al.*, 2011). Intraspecific trait variability, thus, can strongly influence the estimates of community trait composition (Jung *et al.*, 2014). Consequently, it has been strongly advocated to account for intraspecific variability when calculating CWM (Albert *et al.*, 2010).

1.1.4 Soil erosion in agricultural landscapes

Soil erosion is one of the common problems affecting agricultural landscapes, especially in areas subjected to intensive rainfall events. Soil erosion has been intensifying in recent years (Pimentel *et al.*, 1995), and causes reductions in productivity, reaching 50% in some lands (Eswaran *et al.*, 2001). One of the most serious types of soil erosion is the water erosion, which can be distinguished into two forms; (1) loss of topsoil, which is the displacement of soil materials by water, that causes land degradation by removing the top fertile soil layer which affects the crop production by increasing compaction, which decreases the infiltration rates and limits the rooting depth and (2) terrain deformation, that causes the whole area to be affected by rills and gullies (Reganold *et al.*, 1987; Oldeman, 1994; Xu *et al.*, 2013).

During the summer monsoon, the East Asian countries, including South Korea receive a huge amount of rainfall, which impacts both the agriculture and economy (Chen *et al.*, 1988). These rains along with the human activities cause water erosion that produces severe problems in the agricultural landscapes, e.g. land degradation in fields' and downstream sedimentation, flood plains and water bodies, which worsens water quality (Van Oost *et al.*, 2007; Xu *et al.*, 2013). It has been shown that water erosion is responsible for degradation of a total 441 M ha or 59% of the total degraded soil in Asia (Oldeman, 1994).

Preventing and controlling soil erosion can be achieved by reducing the erosive impact of rainfall and maintaining soil infiltration rates, which consequently will prevent surface flow. This can be done using several methods; (1) vegetation restoration, which effectively strengthens soil erosion control, and can be done effectively using vegetated field margins (Zheng, 2006; Wei *et al.*, 2014); (2) field management via crop rotation and tillage practices which can effectively minimize soil erosion, improve water use efficiency and soil carbon sequestration (Raclot & Albergel, 2006; Wang *et al.*, 2010); and (3) by improving the soil stability which will help in soil erosion control in the longer term (Barthès & Roose, 2002).

Field margins can assist in sediment retention by trapping 70-90% of the inflowing sediment, consequently reducing sediment loads to rivers and streams (Duzant *et al.*, 2010). Owens *et al.* (2007), in their study on field margins in agriculture landscape in southwest England, found that the field margins were effective in trapping the coarse sediment fractions, and the amount of sediment was influenced by soil type, slope, land-use and management. Another study done by Heede (1990) on natural vegetated buffer strips in pine forests in Arizona, showed that the vegetated buffer strips trapped 61 times more sediment as compared to sites where buffer strips were missing. Cooper *et al.* (1987), in a study on the efficiency of riparian buffers in controlling soil erosion in two watersheds characterized by >50% forest cover, revealed that the riparian buffers were a sediment sink over 20-year period they studied.

The vegetation of the field margin efficiently traps large heavy particles (Hickey & Doran, 2004). The effectiveness of vegetation cover on sediment trapping and protecting soil against erosion is produced mainly by reducing runoff and by increasing infiltration rate into soil. Moreover, plants protect soil using their roots, which bend the soil particles via the root excretions (Traore *et al.*, 2000; Gyssels *et al.*, 2005; de Baets *et al.*, 2007), by reducing the raindrops' effect on the soil with their canopy (Gray & Sortir, 1996; Durán Zuazo *et al.*, 2008), acting as a physical barrier to change sediment flow at the soil surface (Van Dijk *et al.*, 1996; Lee *et al.*, 2000; Martínez *et al.*, 2006). The spatial distribution of vegetation along the slope is, therefore, an important factor for reducing the sediment runoff (Lavee *et al.*, 1998; Calvo-Cases *et al.*, 2003; Francia Martínez *et al.*, 2006).

One of the factors that influence soil erosion and runoff is slope steepness. Although Abrahams *et al.* (1996) showed that the effect of slope steepness on soil loss is complex, most of the studies didn't show how the slope can affect the soil erosion in detail. These studies, investigated the relation between slope steepness and soil erosion, have been shown that erosion was expected to increase as a function of slope steepness (Zheng, 2006; Fu *et al.*, 2011), as a result of the increase in velocity and volume of surface runoff (Ziadat & Taimeh, 2013). This effect is also affected by other factors like soil properties (Singer & Blackard, 1982), surface conditions (Martínez *et al.*, 2006) and vegetation cover (Singer & Blackard, 1982; Hancock *et al.*, 2015).

1.2. Objectives

The main objective of this thesis is to understand further on the processes governing plant community structure and resulting functioning in agricultural field margins by focusing on describing naturally occurring plant communities of the field margins in the agricultural landscape of Haean-myun catchment in South Korea and how it can affect the ecosystem functioning (e.g. soil stability, soil erosion control), which consequently will help us to understand the functional role of the field margins as an important component of the agro-ecosystem (Fig. 1.2). To achieve this goal, the study addressed three main questions which are:

1. How do local site conditions (margin width, margin management "managed and unmanaged") and landscape-scale land-use (e.g. percentage of non-farmed habitats within several buffer distances) affect field margin's multi-scale plant community structure? (Chapter 2)
2. How do plant functional traits of the species growing on the field margins affect soil stability as a key ecosystem function provided by agricultural landscapes? (Chapter 3)
3. How do the local management and slope degree of the field margins affect ecosystem services in agricultural landscapes (e.g. reduction of local soil erosion)? (Chapter 4)

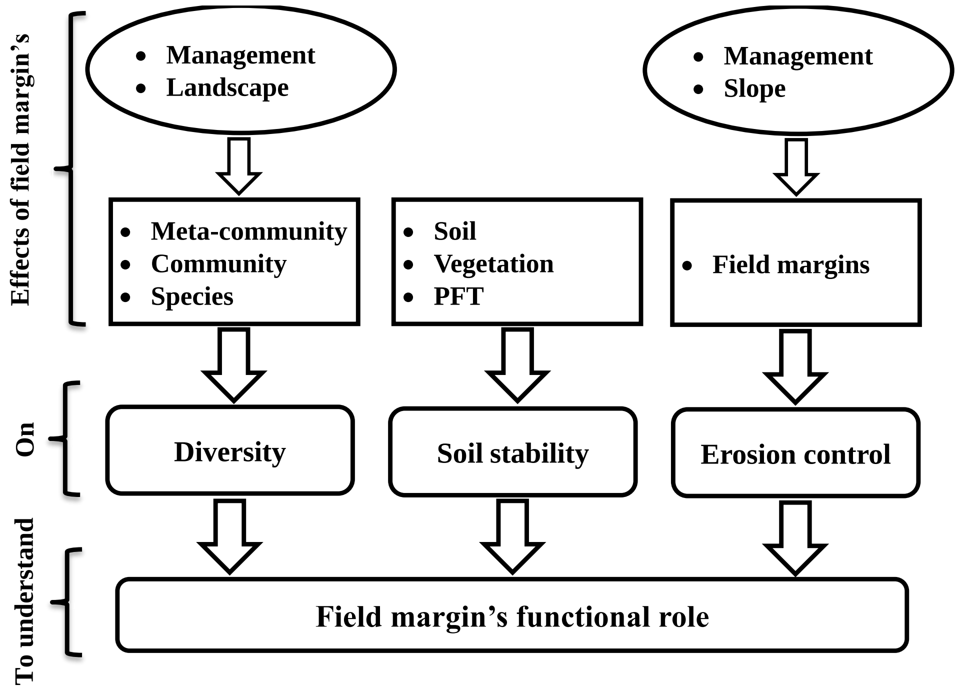

Fig. 1.2. Schematic diagram showing the objectives of the thesis and connections of different parts. The left part of the diagram shows the effect of field margin's local management and the landscape-scale land-use on a multi-scale plant community structure (Chapter 2), the middle part of the diagram shows the effect of soil characteristics, vegetation and plant functional traits (PFTs) on soil stability of the field margins (Chapter 3) and the right part shows the effect of the field margin's management and slope on soil erosion control (Chapter 4).

1.3. Study area

All the fieldwork for this thesis has been conducted in the Haean-myun catchment in South Korea, which is located in the watershed of Soyang Lake close to the Demilitarized Zone (DMZ; 128°05' to 128°11' E, 38°13' to 38°20' N; Fig. 1.3 A). Elevation in the study site varies from 500 to 750 m a.s.l. The mean annual air temperature is 10.5 ºC with minimum monthly temperature of -10 ºC in January and maximum monthly temperature of 27 ºC in August (1999 - 2013). The average precipitation is 1,500 mm, with 70% of the rain falling during the summer monsoon from June to August (Berger *et al.*, 2013).

The total catchment area is 64 km² with 58% of the catchment classified as forested mountains and 30% as agricultural areas (22% dryland fields and 8% rice paddy fields), while the remaining 12% are residential and semi-natural areas including grassland, field margins, riparian areas, channels, and farm roads (Seo *et al.*, 2014). The topography of the research area is characterized by flat areas and moderately steep slopes in the center of the catchment and steep slopes at the catchment edges that are mostly covered by forest. The terrain is highly complex with a variety of different hillslopes and flow directions.

In the Haean-myun catchment, soils are strongly affected by human activities; especially dry fields are modified by the addition of the excavated materials from nearby mountain slopes in order to offset annual erosion losses (Park *et al.*, 2010). Average annual soil erosion rate ranges from 30 to 54 (t $ha^{-1}yr^{-1}$) (Arnhold *et al.*, 2014).

In order to investigate how the local-management and landscape-scale land-use influence the plant communities growing on the field margins (Chapter 2) we surveyed 100 plots well-distributed in the catchment (Fig. 1.3 B). Among 100 plots we chose 30 plots (Fig. 1.3 C) in order to test the effect of the plant functional traits on soil stability (Chapter 3). Finally, for the study about an effect of field margin's local-management and slope degree on soil erosion control (Chapter 4), 12 plots were selected additionally (Fig. 1.3 D).

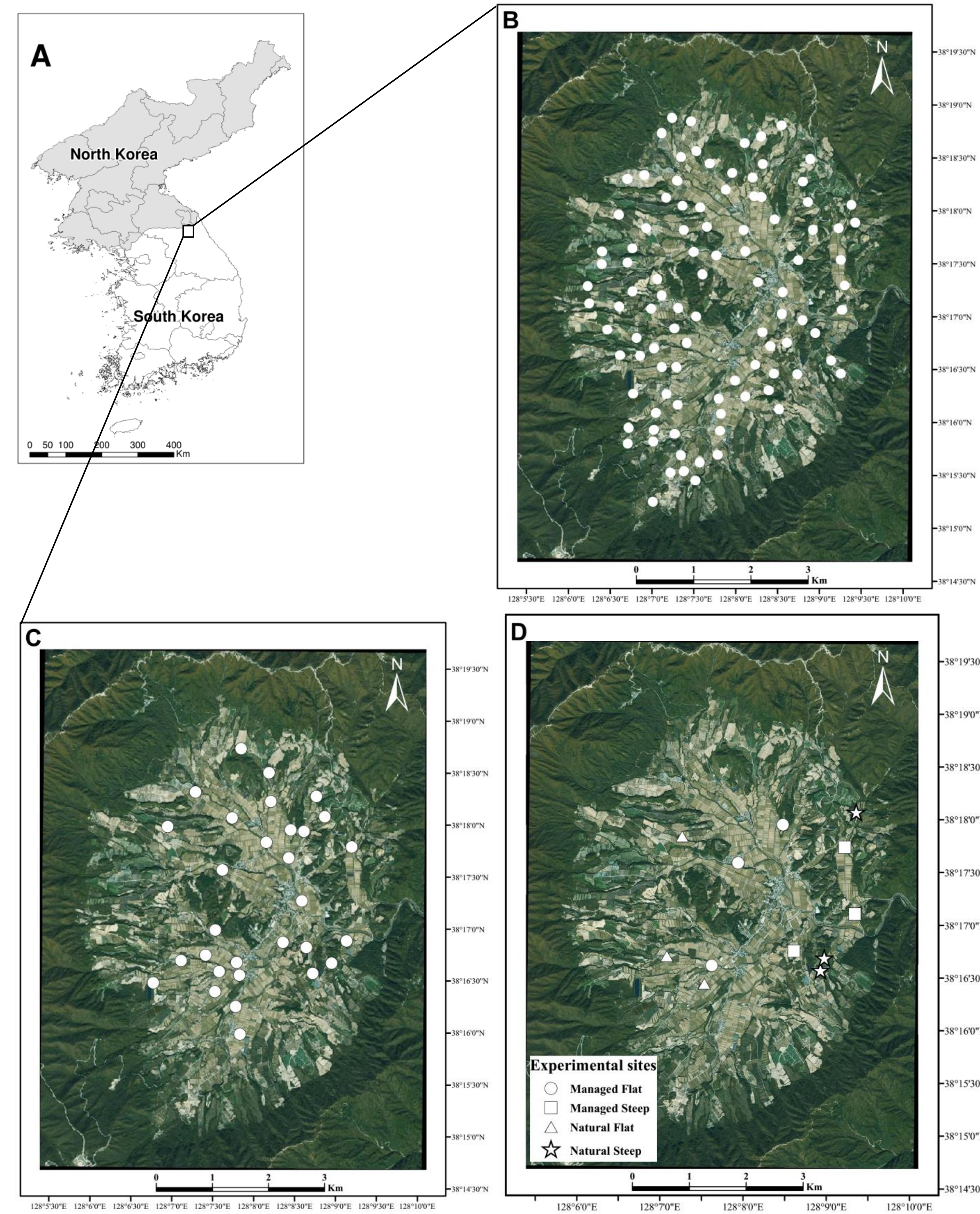

Fig. 1.3. Location of the study area, Haean-myun catchment on the Korean peninsula (A), with the locations of the plots selected for the three studies of this thesis (B, C and D). (B) The 100 sampling plots for the studying the field margins' plant communities (Chapter 2), (C) the 30 sampling plots for the effect of plant functional traits on soil stability (Chapter 3) and (D) the 12 sampling sites for the sediment trapping study (Chapter 4).

1.4. Thesis outline

To answer the research questions formulated in section 1.2, the work was divided into three main parts, outlined as follows:

1.4.1 Diversity of field margins

In this study, we tested how the local-scale management and the landscape-scale land-use influence plant communities of agricultural field margins, by studying multi-facet plant community structure which includes alpha, beta and gamma diversities and species level characteristics such as rareness, growth forms and dispersal types. We addressed two main questions: (1) how does local-scale management vs. landscape-scale land-use influence meta-community, community and species level diversity? and (2) to what extent can species-specific characteristics, such as growth form and dispersal traits, help in explaining this influence?

1.4.2 Effect of plant functional traits on soil stability

In this study, we aimed to integrate vegetation characteristics and functional traits into a model of abiotic soil characteristic effects on soil stability, towards an improved understanding of ecosystem functioning. For this purpose we measured soil stability via soil aggregate stability, soil penetration resistance and soil shear vane strength. First, we tested how well our conceptual model fits data from field margins and how important intraspecific variability is for this fit. Second, we investigated the importance of PFTs in comparison to the influence of abiotic soil characteristics and biotic vegetation characteristics on soil stability. Finally, we asked whether the identified functional effect traits are at the same time important functional response traits. In other words, are the traits that determine the effect on ecosystem functioning the same as those that determine the response of organisms to abiotic conditions?

1.4.3 Effect of field margins on erosion control

The aim of this paper is therefore to investigate how the local management of field margins affects their potential to mitigate the negative effects of soil erosion in a monsoon area. In particular, we compare the amount of sediment trapped between intensively managed field margins (i.e. by cutting) and extensively managed field margins (no management for at least one year). First, we analyze the effects of the two field margin management intensities, on both shallow and steep slopes, on the sediment differences collected after and before the field margins, which is related to the net uptake or release of sediment of the field margin. Second, we analyze the amount of sediment collected within the different field margins, which will give us a wider picture on the amount of sediment that will be trapped by the different types of the field margins.

All the three studies were conducted within the framework of the International Research Training Group TERRECO (Complex TERRain and ECOlogical Heterogeneity) (Kang & Tenhunen, 2010), which aims to assess ecosystem services derived from mountainous landscapes that play an essential role in providing freshwater for large parts of the human population. The TERRECO project consists of a large group of scientists from different fields, who investigate processes related to soils, hydrology, water yield and water quality, agricultural and forest production, biodiversity, and the associated economic gains and losses obtained from those landscapes. The general goal of the research group is the development of an assessment framework that allows the quantitative evaluation of shifts in ecosystem services due to future changes in climate, land use and human population.

This thesis describes how the vegetation of field margins in agricultural landscapes of South Korea can affect important ecosystem services like soil stability and soil erosion control, which simply can illustrate the functional role of the field margins within the landscape. The results of our work provide information that can be used for the parameterization of erosion models like Morgan-Morgan-Finney model (MMF), with respect to erosion prediction in agricultural landscapes. Our findings have also important implications for managing field margins in order to improve the species diversity and consequently several key ecosystem functions which mainly related to soil stability, soil erosion control and water quality in agricultural landscapes. Furthermore, our results can be helpful for future socio-economic studies on the costs and benefits of field margins within agricultural landscapes, which will help in getting the maximum benefits out of it.

1.5. Record of contributions to this thesis

The three studies described in this thesis refer to three different manuscripts. The first manuscript (Chapter 2) is in preparation to be submitted to *Landscape Ecology*, the second manuscript (Chapter 3) got invitation for resubmission at *Plant and Soil*, and the third manuscript (Chapter 4) is submitted to *Journal of Environmental Management* and needs minor revision. The following list specifies the contributions of the individual authors to each manuscript.

Manuscript 1 (Chapter 2):

Authors: Hamada E. Ali, Björn Reineking and Tamara Münkemüller

Title: Drivers of multi-scale plant community structure in agricultural field margins of South Korea

Status: In preparation

Contributions:

H. E. Ali: 75% (concepts, field work, interpretation, discussion and presentation of results, manuscript preparation)

B. Reineking: 10% (concepts, discussion of results, contribution to manuscript preparation)

T. Münkemüller: 15% (concepts, discussion of results, contribution to manuscript preparation)

Manuscript 2 (Chapter 3):

Authors: Hamada E. Ali, Björn Reineking and Tamara Münkemüller

Title: Effects of plant functional traits on soil stability: intraspecific variability matters

Status: Invitation for resubmission

Journal: *Plant and Soil*

Contributions:

H. E. Ali: 70% (concepts, field and lab work, interpretation, discussion and presentation of results, manuscript preparation)

B. Reineking: 10% (concepts, discussion of results, contribution to manuscript preparation)

T. Münkemüller: 20% (concepts, discussion of results, contribution to manuscript preparation)

Manuscript 3 (Chapter 4):

Authors: Hamada E. Ali and Björn Reineking

Title: Extensive management of field margins enhances their potential to mitigate soil erosion

Status: Submitted with minor revision needed.

Journal: *Journal of Environmental Management*

Contributions:

H. E. Ali: 85% (concepts, field work, interpretation, discussion and presentation of results, manuscript preparation)

B. Reineking: 15% (concepts, discussion of results, contribution to manuscript preparation)

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Chapter 2: Drivers of multi-scale plant community structure in agricultural field margins of South Korea

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In preparation to *Landscape Ecology*

Abstract

Field margins are an important component of agricultural landscapes as they support biodiversity and maintain ecosystem functions. Here we use a multi-scale approach to better understand which scales of land management affect which components of plant biodiversity in field margins. In particular, we aim to quantify the effect of local-scale management (distinguishing recently managed and unmanaged field margins) and landscape-scale land-use (measured as percentage of non-farmed habitats) on multi-scale plant community structure at the meta-community level (beta and gamma diversities), community level (alpha diversity), and species level (species rarity, growth form and dispersal). We collected data from one-hundred plots; each divided into three 1 m^2 subplots, from field margins in the Haean-myun catchment, South Korea.

We found that recent local management of field margins resulted in lower alpha diversity but contributed to increased beta and gamma diversity. Abandonment of local management especially increased the diversity of rare species and benefitted the abundance of species characterized by perennial growth forms or abiotic dispersal. At the landscape scale, higher percentages of non-farmed habitats increased the alpha diversity of managed field margins. The positive landscape-scale effect on abundance was highest for annual species, independent of their dispersal mode. We conclude that a multi-scale approach supports an enriched and coherent portrayal of biodiversity responses to land management.

Keywords: Alpha diversity, beta diversity, field margin management, field margin vegetation, landscape context, land-use, non-farmed habitat, plant response.

2.1 Introduction

Changes in land-use practices within agricultural landscapes, such as agriculture intensification and widespread removal of natural vegetation, have led to a decline in biodiversity (Fritch *et al.*, 2011). Diversity in agricultural landscapes is important for the conservation of typical cultural landscapes (Berkes & Davidson-Hunt, 2006; Gao *et al.*, 2013) and their species (Myers *et al.*, 2000; Pimm *et al.*, 2014) but also for ecosystem services such as pest control (Naeem *et al.*, 2012; Reich *et al.*, 2012). However, although a decline of biodiversity in response to land-use changes is well documented (Chapin *et al.*, 2000; Sala *et al.*, 2000) it often remains unclear which types of land management affect which components of biodiversity.

We study field margins in an agricultural landscape in South Korea. The area is subjected to rapid change in land-use, as it has been shifting over the last 40 years towards intensive agriculture, which led to an expansion in farm fields and a reduction in natural areas (Kettering *et al.*, 2012). Within these agricultural landscapes, field margins have an important function for conservation (Marshall, 1988; Moonen & Marshall, 2001), as they provide species refuges as well as feeding and breeding habitats (Ma *et al.*, 2013). Field margins and their diversity also play an important function within the agroecosystem as they promote, for example, soil stability (Pohl *et al.*, 2009; Pérès *et al.*, 2013). In order to reduce species loss and the loss of important ecosystem functions, it is important to understand the effects of different aspects of land management, e.g. local field margin management and landscape structure, on the species growing within the field margins. In the studied field margins we contrast two main types of management. First, local management, which includes cutting, spraying herbicides to remove field margin vegetation, and deciding on field margin width. Second, the landscape-scale land-use management, which can affect the regional species pool and provides opportunities for species dispersal, is here measured as the percentage of non-farmed habitat.

In order to capture key ecological processes in this mosaic landscape—composed of habitable field margins surrounded by uninhabitable agricultural fields—ranging from the meta-community level such as mass and rescue effects to species specific responses (Leibold *et al.*, 2004; Janišová *et al.*, 2014) we study diversity at different scales (e.g. meta-community, community and species levels).

First, at a meta-community scale, it is important to consider the overall diversity (gamma diversity) and the between-plot diversity (beta diversity) because it can explain the influence of the local and landscape managements on the plant community composition, structure and functioning as it reflects different degrees of species composition (Zhang *et al.*, 2014). The importance of the landuse management, e.g. percentage of the non-farmed habitats, to the meta-communities is due to the landuse effect on the regional species pool (Pärtel *et al.*, 1996; Zobel, 1997) in a way that the surrounding habitats represent sources of species that can survive under unfavorable condition (satellite species), which can migrate and increase the diversity of meta-communities' "so called spatial mass effect" (Shmida & Wilson, 1985; Pärtel *et al.*, 2001; Öster *et al.*, 2007).

Second, it is important to look at the community scale (i.e. alpha diversity) which reflects the local diversity of field margins, because alpha diversity is controlled by niche assembly, saturation of local communities, local conditions and biotic interactions (Wright, 1983; Tilman, 2004). Moreover, landuse management is often considered important to alpha diversity, due to environmental species sorting as more heterogeneous areas provide larger niche space, consequently promoting local species coexistence (Svenning, 2001; Phillips *et al.*, 2003).

Finally, the species level, which includes species characteristics, e.g. rarity, growth form and method of seed dispersal, is pivotal in ecological research while studying biodiversity patterns in agricultural landscapes as they can show different responses to both local and landscape managements. The concept of rarity can help in evaluating species interactions within a community, detecting species response to environmental conditions and formulating conservation strategies (Kunin & Gaston, 1997). Prior research showed that common species are mostly responsible for spatial patterns in overall species richness (Lennon *et al.*, 2004). Alahuhta *et al.* (2014), related variations of common and rare species to species sorting, with rare species probably showing pronounced habitat specialization at the species level. While Poos and Jackson (2012) showed that rare species may be more sensitive to environmental conditions, Cao *et al.* (2001) showed that rare species are better than common species in revealing local and land use managements, because common species have wider ranges of tolerance to many environmental conditions, thus making them less suitable as indicators.

We studied also species dispersal, because it is affected by ecological heterogeneity in two different ways; first, it may increase local population sizes, which allows maintaining the distribution and abundance of species within patches by mass or rescue effects (Gonzalez *et al.*, 1998); secondly, in highly heterogeneous meta-communities without asymmetric dispersal, it may decrease diversity by enhancing regional competition (Matthiessen *et al.*, 2010). For studying effect of local and landscape managements on species abundance, it is valuable to group plant species into a limited number of functional groups based on growth form. Growth form are often used to detect species responses to environmental factors such as landscape management (Chapin *et al.*, 1980; Cornelissen *et al.*, 2007), as it can allow to indicate future shifts in community composition, and thus facilitate the prediction of potential loss of certain species due to both local and landscape managements (Dorrepaal, 2007). A series of studies showed that some growth forms such as annuals normally benefit from the management activities (e.g. cutting) but there are other growth forms, e.g. perennials, that occur only at areas with little or no management activities (Noy-Meir & Oron, 2001; Todd & Hoffman, 2009; Papanikolaou *et al.*, 2011).

In this paper, we investigate how local management and landscape-scale land-use influence plant communities of agricultural field margins, by studying multi-facet plant community structure represented by alpha, beta and gamma diversities as well as species level characteristics such as rarity, growth form, and dispersal type. We use data collected from field margins in an agriculture landscape in South Korea. We address two main questions:

(1) How does local-scale management vs. landscape-scale land-use influence meta-community, community and species level diversity?
(2) To what extent can species-specific characteristics, such as growth form and dispersal traits, help in explaining this influence?

2.2 Materials and methods

2.2.1 Study site

The study was conducted in the Haean-myun catchment in South Korea, which is located in the watershed of Soyang Lake close to the Demilitarized Zone (DMZ; 128°05' to 128°11' E, 38°13' to 38°20' N; Fig. 2.1). Elevation in the study site varies from 500 to 750 m a.s.l. The mean annual air temperature is 10.5 ºC, mean monthly temperature varies between -10 ºC in January and 27 ºC in August (1999 - 2013). The average precipitation is 1,500 mm, with 70% of the rain falling during the summer monsoon from June to August (Berger *et al.*, 2013).

The total catchment area is 64 km² with 58% of the catchment classified as forested mountains and 30% as agricultural areas (22% dryland fields and 8% rice paddy fields), while the remaining 12% are residential and seminatural areas including grassland, field margins, riparian areas, channels, and farm roads (Seo *et al.*, 2014). The topography of the research area is characterized by flat areas and moderately steep slopes in the center of the catchment and steep slopes at the catchment edges that are mostly covered by forest.

2.2.2 Data

Plot scale

Our survey of the field margins was conducted between July and August 2011 in 100 sampling plots, covering the whole catchment (Fig. 2.1). In each plot we measured four environmental variables: exposure, slope, width of the field margin, and management type (i.e. "managed" for field margins that had signs of management activities from the ongoing season such as cutting or spraying herbicides and "unmanaged" for field margins that had been left untouched in the season).

For the botanical survey each plot was sampled using three subplots of one square meter per subplot; subplots were 4 m apart from each other (Fig. 2.1). In each subplot, we estimated three different vegetation characteristics: vegetation cover (i.e. the percentage of ground covered by vegetation), species richness (i.e. the number of observed species) and species abundance (i.e. the number of observed individuals / species). The managed field margins were sampled after one month of the management activities.

In our species list all species were classified into dispersal groups of either abiotic (wind- or unassisted dispersal) or biotic dispersal (e.g., by insects, birds, and mammals) and according to their growth form into annual and perennial according to Kim, M *et al.* (2000).

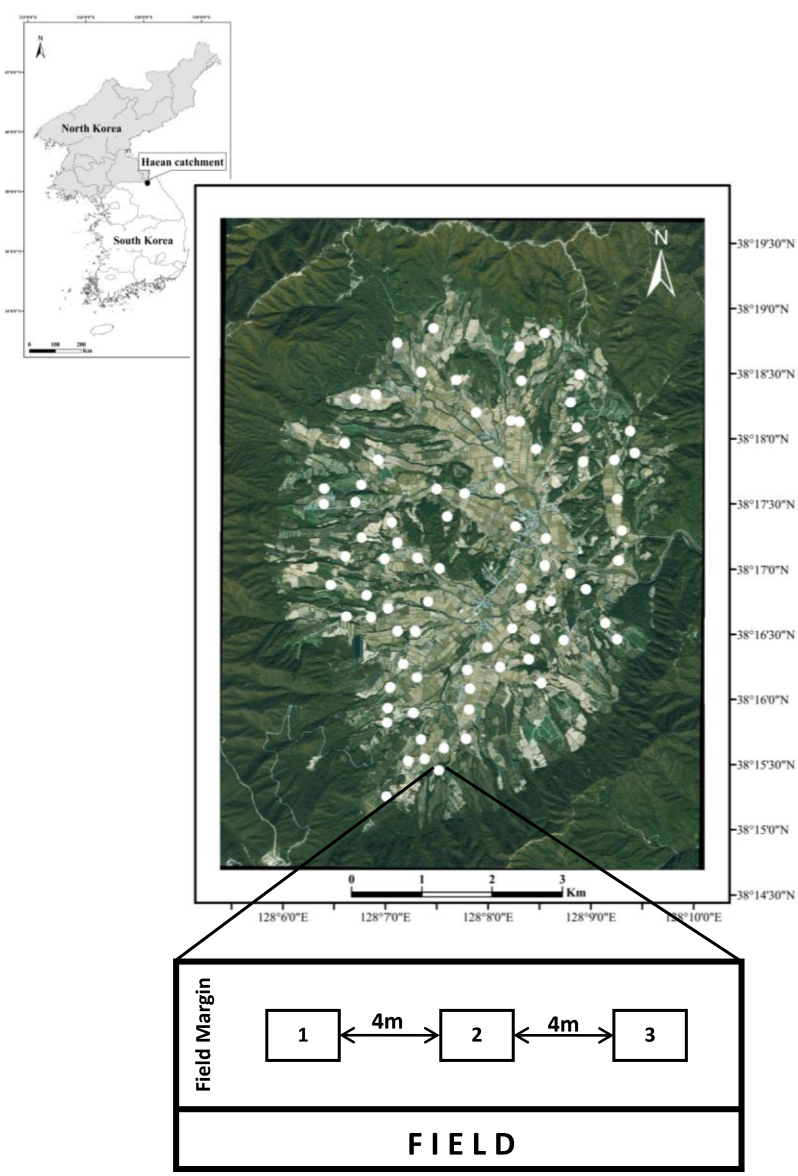

Fig. 2.1. The sampling sites and the sampling design for plant communities in Haean-myun catchment, South Korea. In total, 100 plots (white dots on the map) and 300 subplots were sampled. The lower rectangle shows the sampling design for each plot, with three subplots per plot.

Landscape scale:

To obtain landscape level information on land-use we created buffer zones of 100, 200, 300, 400 and 500 m radii around each plot. Within each of these buffer zones we calculated the percentage of the non-farmed habitats. Non-farmed habitats included field margins, fallows, forest, riparian areas, pasture and grassland in the land-use maps for 2010 provided by Seo *et al.* (2014).

2.2.3 Statistical Analyses

We performed our analyses in three steps: First, we calculated alpha (α) diversity of the 300 subplots, pairwise beta (β) diversity of the 100 plots, each represented by the mean species abundance in the three subplots, and, separately for the managed and unmanaged plots, gamma (γ) diversity. Second, we analyzed the effects of local management and landscape-scale land-use on alpha diversity using linear mixed effects models and on pairwise beta diversity by calculating local contribution to beta diversity (LCBD). Finally, we analyzed the species abundance response to local management and landscape-scale land-use using generalized linear mixed models.

Diversity indices:

We calculated α-diversity for a given subplot using Rényi diversities (Rényi, 1961), defined as:

$$R_{\propto} = \left(-ln \sum_{i=1}^{S} p_i^q\right) / (q-1)$$

where p_i is the proportion of species *i* in the subplot, calculated as the fraction of the total number of individuals in the subplot that belong to species *i*, *S* is the number of species in the subplot, and *q* is the diversity order which determines the sensitivity of $R_{\propto}$ to the effect of species rarity on the diversity estimation. $R_{\propto}$ was calculated for *q* ranging from 0 to 5. With increasing *q*, $R_{\propto}$ is more strongly influenced by dominant species and less by rare species. We calculated α-diversity per plot as the mean α-diversity in its three subplots.

We calculated γ-diversity as the total species richness, separately for the managed and unmanaged plots. To account for the different sample sizes in the managed and unmanaged plots, we used species rarefaction curves.

We followed the approach of Chalmandrier *et al.* (2015) to calculate pairwise β-diversity between each pair of plots as the ratio of γ-diversity of the two plots, and the generalized mean of degree *1- q* of the α-diversities of the two plots (Jost, 2007; Chiu *et al.*, 2014). The γ-diversity of the two plots was the exponential of the Rényi diversity, calculated from the vector of mean relative species abundance over the two plots. The α-diversity of a given plot was the exponential of the Rényi diversity, calculated from the vector of mean relative species abundance over its three subplots.

Influence of landscape and management on alpha diversity

We tested the effect of local man-made activities, including local management (managed or unmanaged) and field margin width, and landscape-scale land-use (% of non-farmed land in the differently sized buffers) on the α-diversity at different diversity order *q* using linear mixed-effect models (LME). The plot ID was included as random effects. To select the best spatial scale at which the α-diversity is best explained, we used the Akaike information criterion (AIC) Akaike (1974) on models fitted with maximum likelihood (ML), choosing as best model the one with lowest AIC; models were then refitted using the restricted maximum likelihood estimation (REML) (Zuur, 2009). To test how the effect sizes of the different fixed effects changed with the diversity order *q*, we extracted the parameter estimates for the variables that significantly affect the α-diversity at different diversity order *q* along with their standard error, then we plotted these estimates for each variable based on the diversity order *q* values, following Crawley (2007).

Influence of landscape and management on beta diversity

To visualize the effect of the local management and landscape-scale land-use on the pairwise β-diversity as a meta-community level, we plotted the pairwise β-diversity of each pair of plots based on the management activities against the percentage of the non-farmed habitats in 300 m radius for each of the diversity order *q*. Moreover, we plotted the β-diversity based on the different field margin management to know how the β-diversity differs according to the field margin's management.

To investigate how exceptional the managed plots were in comparison to unmanaged ones in terms of the abundance differences, we calculated the local contribution to beta diversity (LCBD) which is a comparative indicator to test the ecological uniqueness of the plots for their contributions to total β-diversity (Legendre & De Cáceres, 2013). In this method, the relative contribution of sampling plot *i* to total β-diversity ($LCDB_i$) calculated as follows:

$$LCBD_i = SS_i / SS_{Total}$$

where SS_i represent a genuine partitioning of β-diversity among the plots, which is the squared distance of sampling plot *i* to the centroid of the distribution of plots in species space and SS_{Total} is the total sum of squares of the species abundance data. Species abundance per plot was calculated as the mean abundance in the 3 subplots. Then we mapped the LCBD values using different colors for the managed and unmanaged plots to facilitate the interpretation.

Influence of landscape and management on species abundance:

We analyzed species abundance in response to local management and landscape-scale land-use using Poisson generalized linear mixed models (GLMM) with management, % of non-farmed habitats, growth form, dispersal and the interactions between management and growth form, management and % of non-farmed habitats, growth form and % of non-farmed habitats, management and dispersal and % of non-farmed habitats and dispersal as fixed effects. The subplot ID, nested within plot ID, and species ID were included as random effects. The Akaike's Information Criterion (AIC) (Akaike, 1974) was used to select the best spatial scale at which the species abundance is best explained, which is the model with the lowest AIC.

We calculated the effect of the individual variables and the interactions by including the specified variables and their lower order effects and keeping the other variables to representative values (e.g. their means), which allows us to compute the expected values of the response variable.

All analyses were done using the software R, version 3.1.2 (R Development Core Team, 2014), for the landscape analyses we used the packages: *raster, rgdal, rgeos*. For running the LME and GLMM, we used the package *lme4* (Bates *et al.*, 2014). The calculations of the alpha, gamma diversities and the species rarefaction curve were done using the package *vegan* (Oksanen *et al.*, 2014) and we used the *effect* package (Fox, 2003) to calculate the display effects of the GLMM models.

2.3 Results

2.3.1 Meta-community scale

In our 300 subplots over the Haean-myun catchment, we identified a total of 90 plant species (Table 2.S1) that covered between 50 to 100% of the subplot area. The 44 unmanged field margins were occupied by 68 species, while 81 species were found in the 56 managed field margins. Furthermore, 9 species were restricted only to the natural field margins and 22 species were restricted to the managed field margins (Table 2.S1). The same trend was obtained using the rarefaction curves of the species richness in both the managed and unmanaged plots, as it showed that the managed plots have a higher species richness at the γ-diversity level compared to the unmanaged ones (Fig. 2.2).

The contribution of single plots to β-diversity (LCBD) was spatially not structured (Fig. 2.3a). But it was affected by species richness and local management (Fig. 2.3b). Managed plots with low species richness contributed most to β-diversity (Fig. 2.3a and b). Landscape-level landuse and diversity order *q* had no significant influence on beta diversity (Figs. 2.S1 and 2.S2).

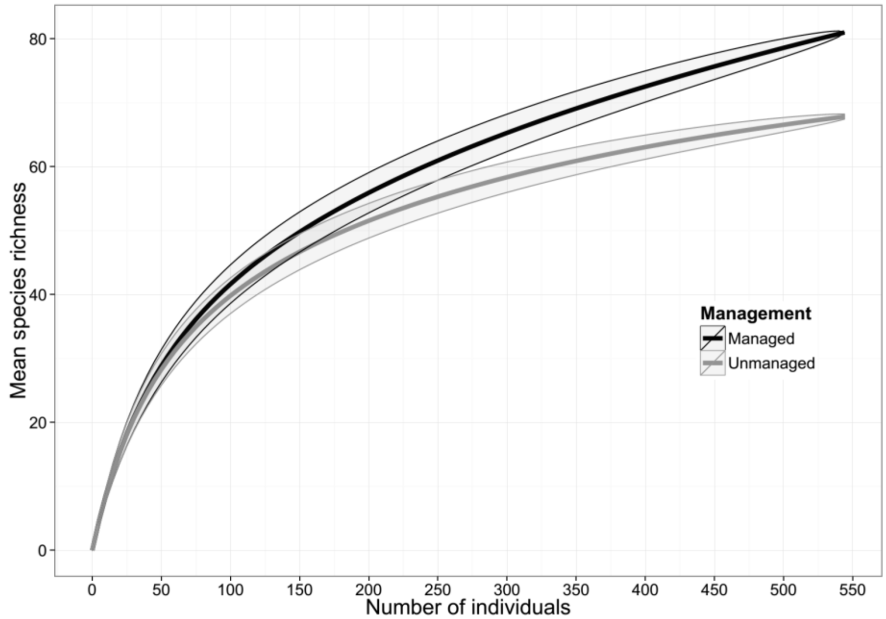

Fig. 2.2. Rarefaction curves of species richness in managed and unmanaged plots.

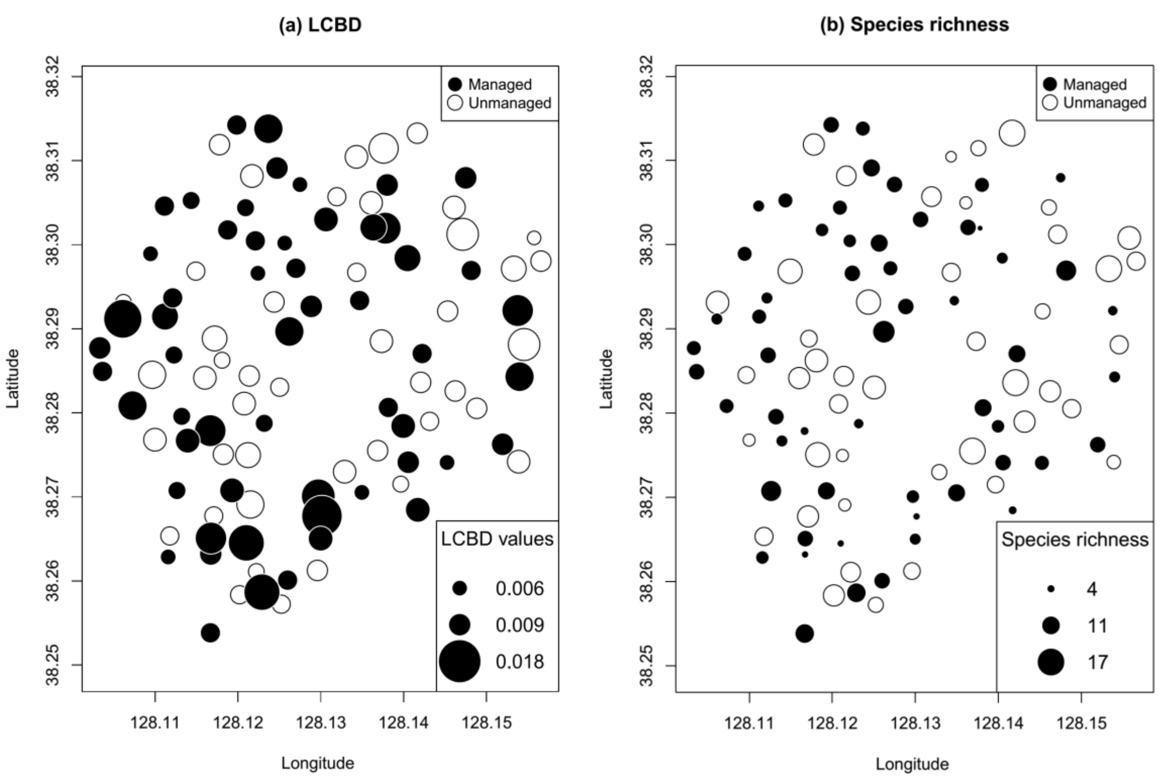

Fig. 2.3. Schematic maps of the 100 study plots showing (a) abundance difference local contribution to beta diversity (LCBD) of each plot and (b) species richness of each plot based on the plot management. Circle sizes are proportional to (a) LCBD and (b) species richness value.

2.3.2 Community scale

At the community scale, α-diversity of the subplots was higher in unmanaged than in managed sites (Fig. 2.4a), thus showing a contrasting pattern to the meta-community scale. The land-use of the surrounding landscape had the strongest effect in a radius of 200 m (Table 2.S2). Interestingly, this landscape-scale land-use only influenced α-diversity of managed local sites. For these sites, α-diversity was increasing with an increasing percentage of non-farmed area in a 200m radius around the plots (Fig. 2.4b). In contrast, α-diversity of unmanaged subplots was not affected by the land-use in the surrounding landscape (Fig. 2.4b).

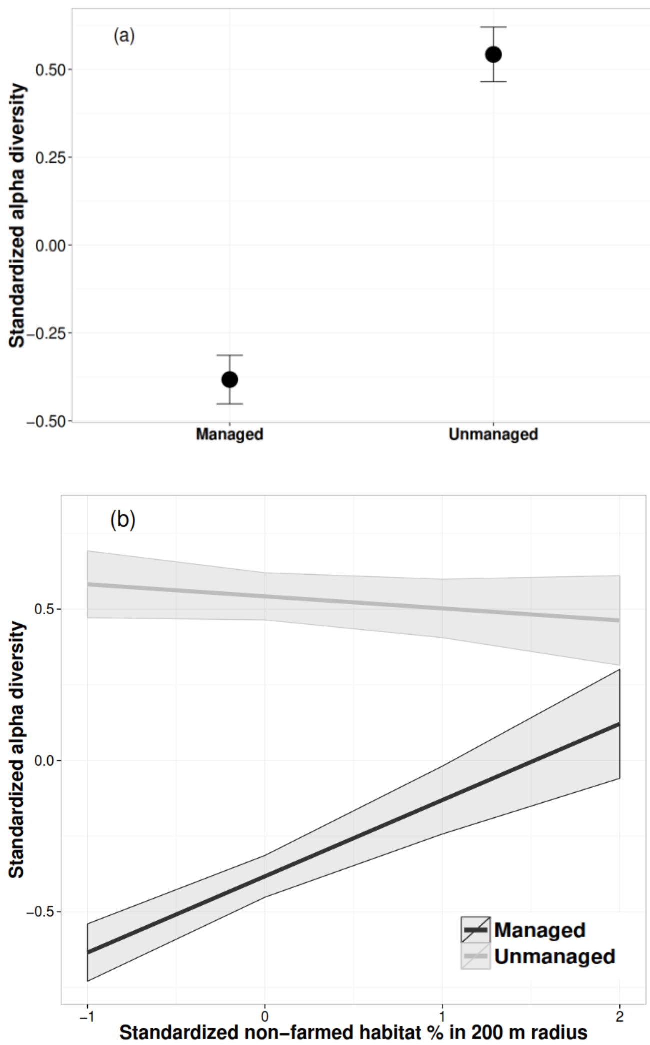

Fig. 2.4. Effect display for (a) management and (b) non-farming % in 200 m radius on alpha diversity.

2.3.3 Species abundances

Based on the lowest AIC values, we chose a radius of 300 m as the best spatial scale to describe the effects on the species abundance (Table 2.S3). Species abundances depended on the interaction of management and land-use with species' dispersal type and growth form (Fig. 2.5, Table 2.S3). Species with abiotic dispersal were generally more abundant than those with biotic dispersal, especially if plots were locally unmanaged (Fig. 2.5a). In contrast, local management had no significant influence on the abundance of species with biotic dispersal (Fig. 2.5a). The non-farmed habitat increased abundances of species independent of their dispersal type (Fig. 2.5b, Table 2.S3).

Annual species were generally more abundant than perennial species. The abundance of annual species was not significantly affected by local management (Fig. 2.5c), but annual species benefitted from landscape-scale non-farmed habitat (Fig. 2.5d). In contrast, perennial species were significantly more abundant in unmanaged plots (Fig. 2.5c) but did not respond to landscape-scale land-use (Fig. 2.5d).

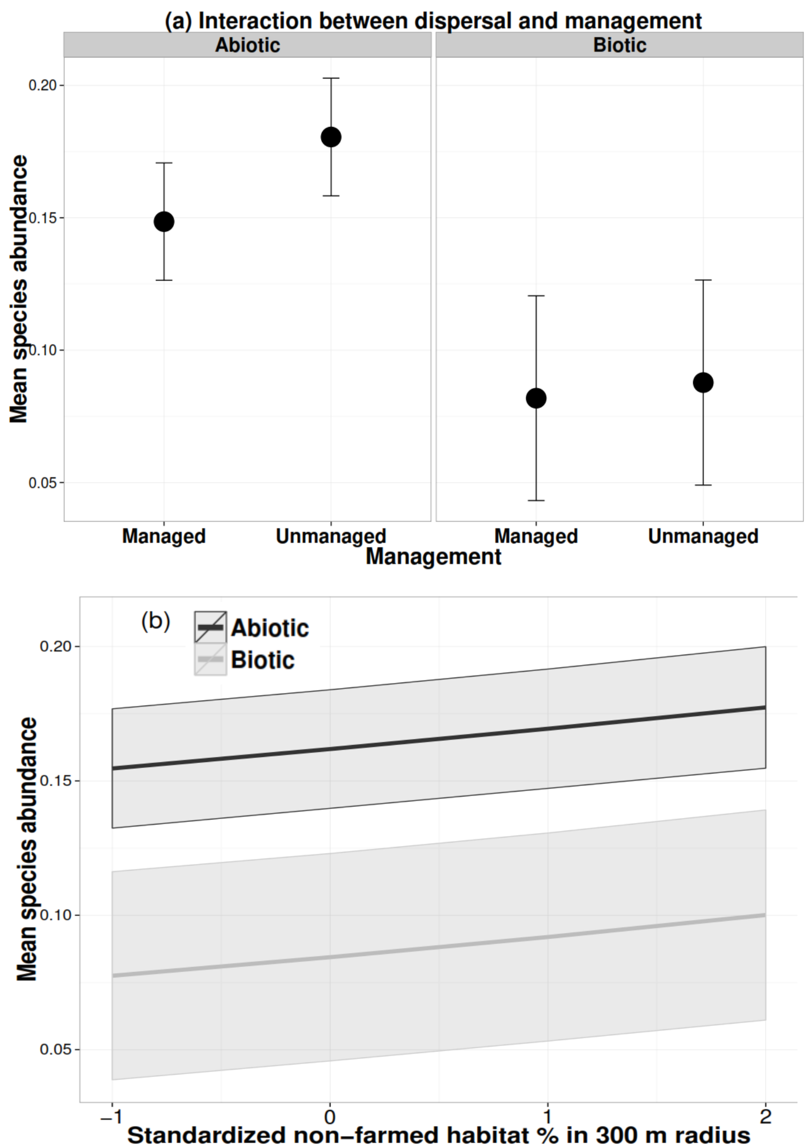

Fig. 2.5. Differences in species abundance based on (a) management and seed dispersal, (b) percentage of non-farmed habitat in 300 m radius and seed dispersal, (c) management and growth form, (d) percentage of non-farmed habitat in 300 m radius and growth form.

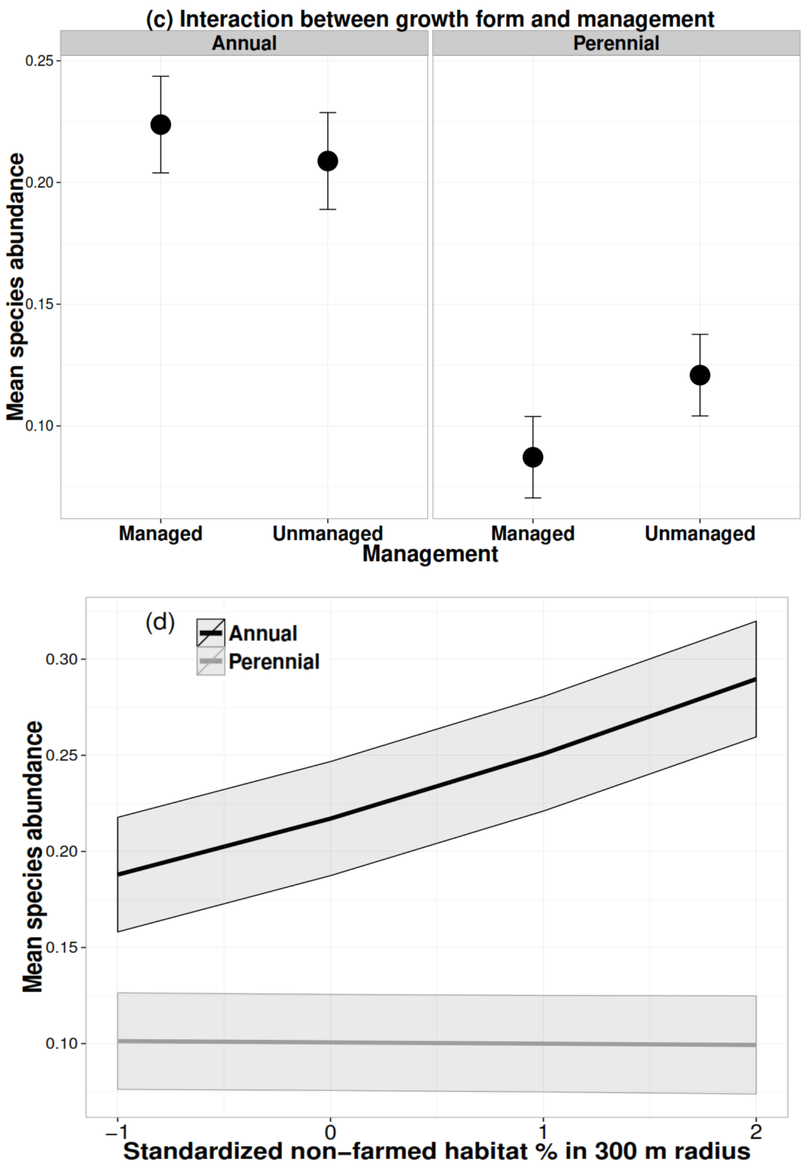

Fig. 2.5 (cont.). Differences in species abundance based on (a) management and seed dispersal, (b) percentage of non-farmed habitat in 300 m radius and seed dispersal, (c) management and growth form, (d) percentage of non-farmed habitat in 300 m radius and growth form.

The order parameter q of the diversity index affects how strongly rare species contribute to the diversity index; for q = 0, all species contribute the same, irrespective of their abundance; for higher values of q, more abundant species increasingly dominate the value of the diversity. The effect of unmanaged field margin on the α-diversity in the field margins was decreasing with larger values for q, suggesting that in particular rare species benefit from unmanaged field margins (Fig. 2.6a). In contrast, the effect of the percentage of non-farmed habitat in 200 m radius did not vary significantly with the order parameter q (Fig. 2.6b).

Overall, we found that abandonment of local management in field margins positively influenced α-diversity and especially the diversity of species that are rare and the abundance of species that are characterized by abiotic dispersal and perennial growth forms. In contrast, local management of field margins resulted in lower alpha diversity and contributed to high β-diversity. The availability of landscape-scale non-farmed habitats influenced especially the diversity of managed field margins by increasing alpha diversity.

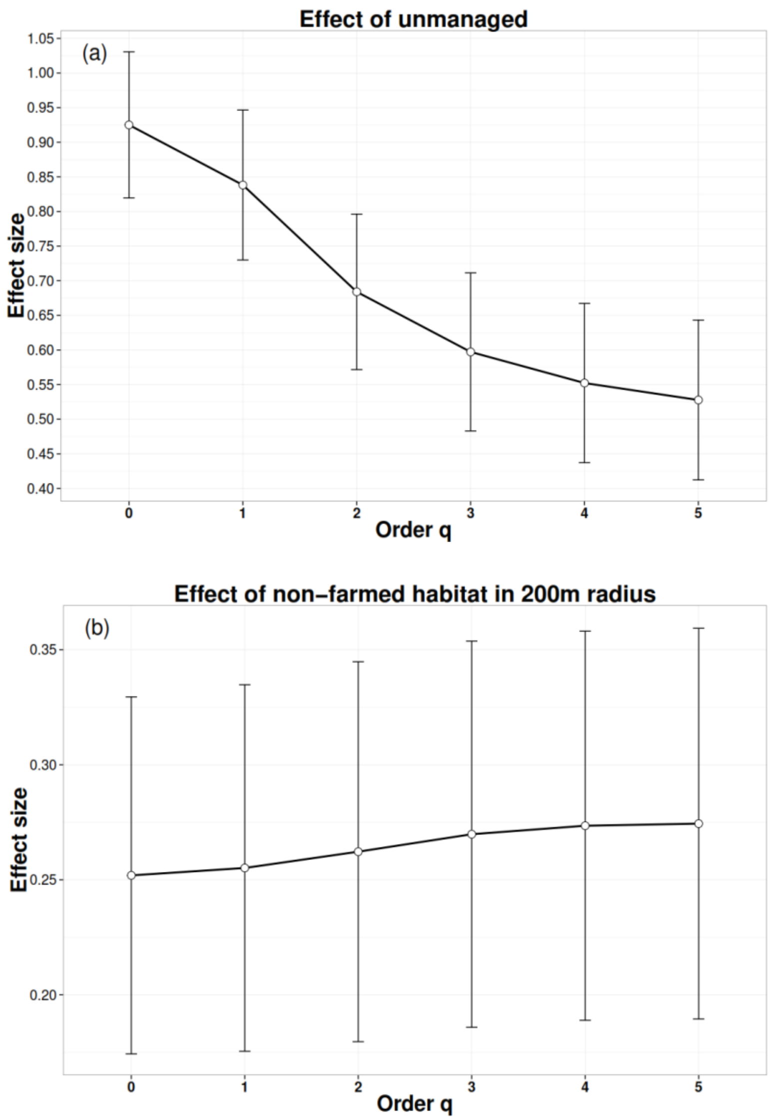

Fig. 2.6. Effect size of (a) Unmanaged management and (b) Percentage of non-farmed habitat in 200 m radius on alpha diversity at different diversity order *q*.

2.4 Discussion

Local-scale management and landscape-scale land-use are important factors driving diversity of plant communities in agricultural landscapes. Here, we apply a multi-scale approach to disentangle these effects at the meta-community scale (β and γ-diversities), the community scale (α- diversity) and the species level for field margins in South Korea. Our results highlight the differential effects of local-scale management and landscape-scale land-use on plant diversity at different scales depending on species characteristics such as rarity, growth form and dispersal.

Our results showed that the local management and landscape-scale land-use have differential effects, as local management influences mostly the rare species (Fig. 2.6a), those with abiotic dispersal (Fig. 2.5a) and with perennial growth form (Fig. 2.5c). In contrast, landscape-scale land-use influences more the diversity of species in the managed plots (Fig. 2.4b) and the abundance of annual species (Fig. 2.5d). We interpret these results such that the plant communities of the field margins respond to a gradient of degradation, in which increasing degradation causes a decrease in perennial and rare species and an increase in annual and dominant species. Our study support the idea that annual species increase with disturbance (Wilson & Tilman, 1991), as due to the local management activities, more gaps will be produced allowing the annuals species which can rapidly use the resources to colonize and establish in the managed plots (Grime, 1974). Moreover, these different responses can be due to the different functional response of certain species traits as it can be associated to both environmental filtering and biotic interactions (Gross *et al.*, 2009; de Bello *et al.*, 2012). The high contribution of the managed plots to total β-diversity (Fig. 2.3a), reveals that these plots are degraded and species poor in compare to the unmanaged ones (Legendre, 2014), which we can easily notice in the species richness map (Fig. 2.3b) as the managed sites that has high LCBD, showed to have lower species richness.

Managed field margins were found to have a lower α-diversity (Fig. 2.4a) and have a positive relation to landscape-scale land-use (Fig. 2.4b), suggesting that if field margins are managed they should at least have access to non-farmed habitats in the surroundings to provide seed sources. These results go in line with other studies that showed the pivotal role of the complexity of the surrounding land-use in maintaining the plant diversity in agricultural landscapes (Weibull & Östman, 2003; Liira *et al.*, 2008; Poggio *et al.*, 2010; Ma *et al.*, 2013), as the increasing in the landscape heterogeneity act as a source for species dispersal into the field margins (Weibull & Östman, 2003). In their study on the field margins of South Korea, Kang *et al.* (2013) showed that the species of field margins were mostly affected by habitat connectivity, which goes in line with our results but in contrast to our findings the local management were not affecting the species richness, which may partly be due to their lower sample size, as they collected data from only 12 field margins using three transects at each field margin.

Finally, managed field margins with little surrounding habitats are most degraded with low α-diversity (Fig. 2.4b). These results agree with the intermediate landscape complexity hypothesis, which predicts that local management in agricultural landscapes have an effect on species diversity in simple but not complex landscapes (Batáry *et al.*, 2011). In simple landscapes, the lack of habitat heterogeneity surrounding plots provides a limited pool of species that may be able to withstand or counterbalance, species loss from the managed plots (MacArthur & Wilson, 1967; Pärtel *et al.*, 1996; Janišová *et al.*, 2014). In contrast, in complex landscapes, the agricultural landscapes are characterized by a high level of immigration of organisms from the surrounding habitats (e.g. non-farmed land) (Bianchi *et al.*, 2006; Ricketts *et al.*, 2008; Tscharntke *et al.*, 2008) which can overcome the effects of local management practices (Kremen *et al.*, 2004; Tscharntke *et al.*, 2005).

At the meta-community scale, the results of γ-diversity (overall diversity) showed that the species richness in managed field margins was higher than in the unmanaged ones (Fig. 2.2). This pattern may be due to a meta-community overall richer in annual species that benefit from the creation of early succesional stages with open soil as a consequence of the local management.

Conclusion

As agricultural landscapes occupy around 50% of the earth's land surface (USDA, 2013), it is pivotal to sustain and maintain the biodiversity in these system to improve the ecosystem functioning. In the current study, we showed how important the local-management of the field margins and the surrounding landscape-scale land-use are in maintaining the diversity in the agricultural landscapes by studying the response of the plant communities at multi-scales. In conclusion, we emphasize the importance of the multi-scale approach as it supports an enriched and coherent portrayal of biodiversity responses to local and landscape-scale managements. As the local management is mainly affecting the plots that have no surrounding habitats, it is important that if the field margins are managed they should at least have access to non-farmed habitats in the surroundings to help increasing the plant diversity via species dispersal.

2.5 Acknowledgements

This work is part of the International Research Training Group ''Complex TERRain and ECOlogical Heterogeneity" (TERRECO) (GRK 1565/1) funded by the German Research Foundation (DFG). We thank Bumsuk Seo for supporting us in the field work, Donguk Han for identifying the plant species, Dowon Lee for his comments and suggestions on our field protocol and John Tenhunen for his comments and coordination of the TERRECO fieldwork.

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2.7 Supplementary materials

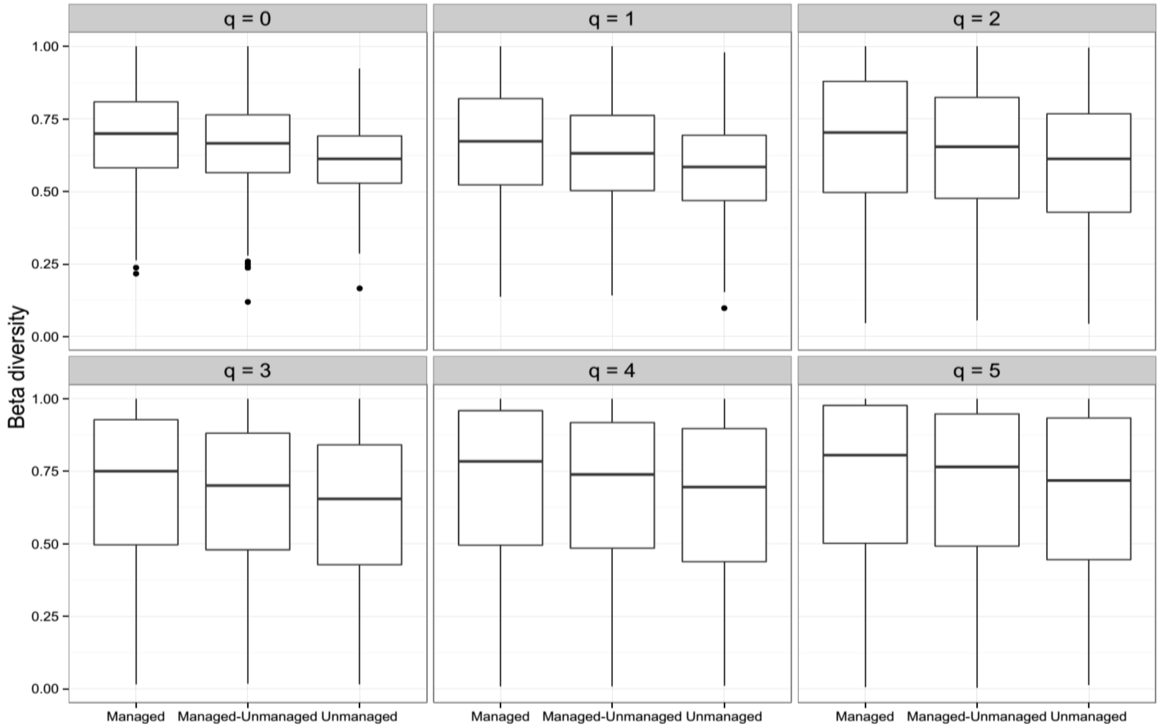

Fig. 2.S1. Effect of management on beta diversity at different diversity order *q*.

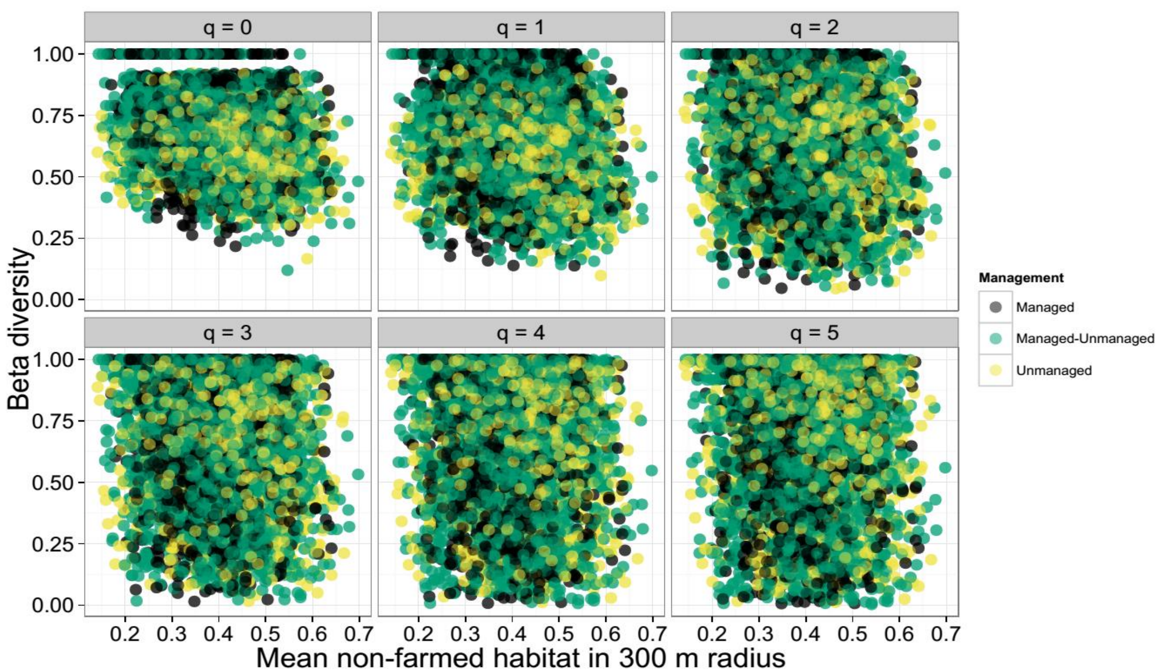

Fig. 2.S2. Effect of percentage of non-farmed habitat in 300 m radius on beta diversity at different diversity order *q*.

Table 2.S1. List of the 90 species recorded during the field margin survey along with species growth form, mean of seed dispersal and species relative abundance.

Species Latin Name	Korean Common Name	Family	Growth form	Dispersal	Relative Abundance (%)	Comments
Acalypha australis L.	깨풀	Euphorbiaceae	Annual	Abiotic	0.21	Restricted to managed margins
Ambrosia artemisiifolia L.		Asteraceae	Annual	Abiotic	0.62	
Artemisia apiacea Hance ex Walp.	개사철쑥	Asteraceae	Perennial	Abiotic	1.08	
Artemisia feddei H.Lev. & Vaniot	뺑쑥	Asteraceae	Perennial	Abiotic	0.1	Restricted to managed margins
Artemisia princeps Pamp.	쑥	Asteraceae	Perennial	Abiotic	0.62	
Artemisia sp	쑥	Asteraceae	Perennial	Abiotic	11.23	
Arundinella hirta (Thunb.) Koidz.	새	Poaceae	Perennial	Abiotic	0.1	
Aster pilosus Willd.	미국쑥부쟁이	Asteraceae	Perennial	Biotic	0.1	
Aster tataricus L.f.	개미취	Asteraceae	Perennial	Abiotic	0.21	Restricted to unmanaged margins
Astilbe rubra Hook.f. & Thomson var. *rubra*	노루오줌	Saxifragaceae	Perennial	Abiotic	0.1	Restricted to managed margins
Bidens frondosa L.	미국가막사리	Asteraceae	Annual	Biotic	2.63	
Calystegia sepium var. *japonicum* (Choisy) Makino	메꽃	Convolvulaceae	Perennial	Abiotic	2.99	
Chamaecrista nomame (Siebold) H.Ohashi	차풀	Fabaceae	Perennial	Abiotic	0.62	
Chelidonium majus var. *asiaticum* (Hara) Ohwi	애기똥풀	Papaveraceae	Perennial	Abiotic	0.26	
Chenopodium ficifolium Smith	좀명아주	Chenopodiaceae	Annual	Abiotic	0.98	
Clinopodium chinense var. *parviflorum* (Kudo) Hara	층층이꽃	Lamiaceae	Perennial	Biotic	0.05	Restricted to managed margins
Commelina communis L.	닭의장풀	Commelinaceae	Annual	Abiotic	7.99	
Conyza canadensis (L.) Cronquist	망초	Asteraceae	Annual	Abiotic	2.83	
Crepidiastrum sonchifolium (Bunge) Pak & Kawano	고들빼기	Asteraceae	Annual	Biotic	0.05	Restricted to unmanaged margins
Cyperus microiria Steud.	금방동사니	Cyperaceae	Annual	Abiotic	1.03	
Dendranthema boreale (Makino) Ling ex Kitam.	산국	Asteraceae	Perennial	Abiotic	0.1	Restricted to unmanaged margins
Dendranthema zawadskii var. *latilobum* (Maxim.) Kitam.	구절초	Asteraceae	Perennial	Abiotic	0.05	Restricted to managed margins
Digitaria ciliaris (Retz.) Koel.	바랭이	Poaceae	Annual	Biotic	2.37	
Echinochloa crusgalli (L.) P.Beauv.	돌피	Poaceae	Annual	Abiotic	2.32	
Equisetum arvense L.	쇠뜨기	Equisetaceae	Perennial	Abiotic	3.5	
Erigeron strigosus Muhl.	주걱개망초	Asteraceae	Perennial	Abiotic	4.02	
Eupatorium japonicum Thunb.	등골나물	Asteraceae	Perennial	Abiotic	0.77	
Eupatorium sp	등골나물 sp.	Asteraceae	Perennial	Abiotic	0.72	
Fallopia dumetorum (L.) Holub	닭의덩굴	Polygonaceae	Annual	Abiotic	0.15	Restricted to managed margins
Festuca arundinacea Schreb.	큰김의털	Poaceae	Perennial	Biotic	1.13	
Galinsoga ciliata (Raf.) S.F.Blake	털별꽃아재비	Asteraceae	Annual	Biotic	0.1	Restricted to managed margins
Geranium sibiricum L.	쥐손이풀	Geraniaceae	Perennial	Abiotic	1.75	
Glycine soja Siebold & Zucc.	돌콩	Fabaceae	Annual	Abiotic	3.5	
Humulus japonicus Sieboid & Zucc.	환삼덩굴	Cannabaceae	Annual	Abiotic	6.44	
Hypericum ascyron L.	물레나물	Clusiaceae	Perennial	Abiotic	0.05	Restricted to managed margins

Species Latin Name	**Korean Common Name**	**Family**	**Growth form**	**Dispersal**	**Relative Abundance (%)**	**Comments**
Hypericum sp	고추나물 sp.	Clusiaceae	Perennial	Abiotic	0.15	Restricted to managed margins
Impatiens nolitangere L. var. nolitangere	노랑물봉선	Balsaminaceae	Annual	Abiotic	0.1	Restricted to unmanaged margins
Impatiens textori var. *koreana* Nakai	흰물봉선	Balsaminaceae	Annual	Abiotic	0.05	Restricted to managed margins
Impatiens textori var. *textori*	물봉선	Balsaminaceae	Annual	Abiotic	1.03	
Isodon japonicus (Burm.) Hara	방아풀	Lamiaceae	Perennial	Abiotic	0.05	Restricted to managed margins
Lactuca indica L.	왕고들빼기	Asteraceae	Perennial	Abiotic	1.03	
Leonurus japonicus Houtt.	익모초	Lamiaceae	Annual	Abiotic	1.29	
Lespedeza bicolor Turcz.	싸리	Fabaceae	Perennial	Abiotic	0.93	
Lysimachia clethroides Duby	큰까치수염	Primulaceae	Perennial	Abiotic	0.05	Restricted to unmanaged margins
Lysimachia vulgaris var. *davurica* (Ledeb.) R.Kunth	좁쌀풀	Primulaceae	Perennial	Abiotic	0.15	
Mazus pumilus (Burm.f.) Steenis	주름잎	Scrophulariaceae	Annual	Abiotic	0.05	Restricted to managed margins
Mentha piperascens (Malinv.) Holmes	박하	Lamiaceae	Perennial	Abiotic	0.26	
Metaplexis japonica (Thunb.) Makino	박주가리	Asclepiadaceae	Annual	Abiotic	2.83	
Oenanthe javanica (Blume) DC.	미나리	Apiaceae	Perennial	Biotic	0.1	
Oenothera biennis L.	달맞이꽃	Onagraceae	Perennial	Abiotic	3.25	
Onoclea sensibilis var. *interrupta* Maxim.	야산고비	Onocleaceae	Perennial	Biotic	0.1	Restricted to managed margins
Oxalis corniculata L.	괭이밥	Oxalidaceae	Annual	Abiotic	0.21	
Oxalis stricta L.	선괭이밥	Oxalidaceae	Annual	Abiotic	0.1	
Panicum dichotomiflorum Michx.	미국개기장	Poaceae	Annual	Biotic	0.31	
Patrinia scabiosaefolia Fisch. ex Trevir.	마타리	Valerianaceae	Perennial	Abiotic	0.21	
Persicaria longiseta (Bruijn) Kitag.	개여뀌	Polygonaceae	Annual	Abiotic	0.31	Restricted to managed margins
Persicaria nepalensis (Meisn.) H.Gross	산여뀌	Polygonaceae	Annual	Abiotic	2.11	
Persicaria perfoliata (L.) H.Gross	며느리배꼽	Polygonaceae	Annual	Abiotic	1.96	
Persicaria sagittata (L.) H.Gross ex Nakai	미꾸리낚시	Polygonaceae	Annual	Abiotic	0.15	Restricted to managed margins
Persicaria senticosa (Meisn.) H.Gross ex Nakai var. *senticosa*	며느리밑씻개	Polygonaceae	Annual	Biotic	0.05	Restricted to managed margins
Persicaria thunbergii (Siebold & Zucc.) H.Gross ex Nakai	고마리	Polygonaceae	Annual	Abiotic	0.93	
Persicaria vulgaris Webb & Moq.	봄여뀌	Polygonaceae	Annual	Abiotic	3.92	
Petasites japonicus (Siebold & Zucc.) Maxim.	머위	Asteraceae	Annual	Abiotic	0.1	
Phleum pratense L.	큰조아재비	Poaceae	Perennial	Biotic	0.05	Restricted to managed margins
Phragmites japonica Steud.	달뿌리풀	Poaceae	Perennial	Abiotic	1.18	
Picris hieracioides var. *koreana* Kitam.	쇠서나물	Asteraceae	Perennial	Biotic	0.15	
Plantago asiatica L.	질경이	Plantaginaceae	Perennial	Abiotic	2.01	
Pteridium aquilinum var. *latiusculum* (Desv.) Underw. ex Hell.	고사리	Polypodiaceae	Perennial	Abiotic	0.15	Restricted to unmanaged margins
Pueraria lobata (Willd.) Ohwi	칡	Fabaceae	Perennial	Biotic	0.72	
Robinia pseudoacacia L.	아까시나무	Fabaceae	Perennial	Abiotic	0.26	
Rorippa palustris (Leyss.) Besser	속속이풀	Brassicaceae	Annual	Abiotic	0.31	
Rubus crataegifolius Bunge	산딸기	Rosaceae	Perennial	Biotic	2.83	

Species Latin Name	Korean Common Name	Family	Growth form	Dispersal	Relative Abundance (%)	Comments
Rubus oldhamii Miq.	모시물통이	Rosaceae	Perennial	Biotic	0.21	
Rubus phoenicolasius Maxim.	곰딸기	Rosaceae	Perennial	Biotic	0.1	
Rudbeckia *laciniata* var. *hortensis* Bailey	겹삼잎국화	Asteraceae	Perennial	Abiotic	0.05	Restricted to unmanaged margins
Rumex crispus L.	소리쟁이	Polygonaceae	Perennial	Abiotic	0.05	Restricted to unmanaged margins
Sanguisorba officinalis L.	오이풀	Rosaceae	Perennial	Abiotic	0.15	
Setaria faberii Herrm.	가을강아지풀	Poaceae	Perennial	Abiotic	3.14	
Setaria sp	강아지풀 sp.	Poaceae	Annual	Abiotic	1.03	
Setaria viridis (L.) P.Beauv. var. viridis	강아지풀	Poaceae	Annual	Abiotic	0.26	Restricted to managed margins
Solanum nigrum L. var. *nigrum*	까마중	Solanaceae	Annual	Biotic	0.05	Restricted to managed margins
Sonchus brachyotus DC.	사데풀	Asteraceae	Perennial	Abiotic	0.21	Restricted to managed margins
Spiraea salicifolia L.	꼬리조팝나무	Rosaceae	Perennial	Biotic	0.05	
Spodiopogon sibiricus Trin.	큰기름새	Poaceae	Perennial	Abiotic	0.26	
Stachys japonica Miq.	석잠풀	Lamiaceae	Perennial	Biotic	1.75	
Stellaria media (L.) Vill.	별꽃	Caryophyllaceae	Annual	Abiotic	0.52	
Trifolium sp	토끼풀 sp.	Fabaceae	Annual	Abiotic	0.31	
Vicia japonica A.Gray	넓은잎갈퀴	Fabaceae	Perennial	Biotic	1.08	
Zizania latifolia (Griseb.) Turcz. ex Stapf	줄	Poaceae	Perennial	Abiotic	0.41	Restricted to unmanaged margins
Zoysia japonica Steud.	잔디	Poaceae	Perennial	Biotic	0.1	Restricted to managed margins

Table 2.S2. The linear mixed-effect models (LME) for different alpha diversity order *q* values at non-crop % in 200 m radius (*N* = 100). Significant variables are in bold.

Model	AIC	Fixed Effect	Value	SE	*t*	*P*
q = 0	793.10	**Intercept**	**-0.383**	**0.069**	**-5.546**	**<0.001*** **
		Unmanaged plots	**0.925**	**0.106**	**8.765**	**<0.001*** **
		Width	0.016	0.053	0.300	0.765
		Non-farmed % at 200 m	**0.252**	**0.078**	**3.248**	**<0.001*** **
		Unmanaged : Non-farmed	**-0.292**	**0.103**	**-2.822**	**0.005** **
q = 1	808.56	**Intercept**	**-0.353**	**0.071**	**-4.976**	**<0.001*** **
		Unmanaged plots	**0.838**	**0.108**	**7.737**	**<0.001*** **
		Width	-0.033	0.054	-0.605	0.546
		Non-farmed % at 200 m	**0.255**	**0.080**	**3.204**	**0.002** **
		Unmanaged : Non-farmed	-0.196	0.106	-1.849	0.066
q = 2	829.80	**Intercept**	**-0.286**	**0.073**	**295.000**	**<0.001*** **
		Unmanaged plots	**0.684**	**0.112**	**295.000**	**<0.001*** **
		Width	-0.055	0.056	295.000	0.329
		Non-farmed % at 200 m	**0.262**	**0.083**	**295.000**	**0.002** **
		Unmanaged : Non-farmed	-0.182	0.110	295.000	0.098
q = 3	839.4	**Intercept**	**-0.246**	**0.075**	**295.000**	**<0.001*** **
		Unmanaged plots	**0.597**	**0.114**	**295.000**	**<0.001*** **
		Width	-0.060	0.057	295.000	0.290
		Non-farmed % at 200 m	**0.270**	**0.084**	**295.000**	**0.001** **
		Unmanaged : Non-farmed	-0.198	0.112	295.000	0.078
q = 4	843.91	**Intercept**	**-0.226**	**0.075**	**-2.998**	**0.003** **
		Unmanaged plots	**0.552**	**0.115**	**4.800**	**<0.001*** **
		Width	-0.063	0.057	-1.101	0.272
		Non-farmed % at 200 m	**0.274**	**0.085**	**3.235**	**0.001** **
		Unmanaged : Non-farmed	-0.210	0.113	-1.859	0.064
q = 5	846.27	**Intercept**	**-0.214**	**0.076**	**-2.838**	**0.005** **
		Unmanaged plots	**0.528**	**0.116**	**4.569**	**<0.001*** **
		Width	-0.065	0.058	-1.127	0.261
		Non-farmed % at 200 m	**0.274**	**0.085**	**3.233**	**<0.001*** **
		Unmanaged : Non-farmed	-0.215	0.113	-1.903	0.058

Significance codes: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$. Statistically significant variables are indicated in bold

Table 3.S3. The generalized linear mixed-effect model (GLMM) for the species abundance response at non-crop % in 200 m radius (*N* = 27000). Significant variables are in bold. The best model according to the lowest AIC value is highlighted in grey.

Model	AIC	Fixed Effect	Value	SE	*z*	*P*
100 m	66246	**(Intercept)**	**-1.339**	**0.309**	**-4.336**	**<0.001*** **
		Unmanaged plots	-0.049	0.052	-0.945	0.344
		Perennial species	**-0.958**	**0.387**	**-2.477**	**0.013***
		Non-farmed % at 100 m radius	0.018	0.031	0.596	0.551
		Biotic species	-0.594	0.442	-1.345	0.179
		Unmanaged : Perennial	**0.411**	**0.033**	**12.265**	**<0.001*** **
		Unmanaged : Non-farmed % at 100 m radius	0.096	0.052	1.840	0.066
		Perennial : Non-farmed % at 100 m radius	**-0.073**	**0.017**	**-4.240**	**<0.001*** **
		Unmanaged : Biotic	**-0.127**	**0.047**	**-2.675**	**0.007** **
		Non-farmed % at 100 m radius : Biotic	0.041	0.024	1.726	0.084
200 m	66208	**(Intercept)**	**-1.346**	**0.306**	**-4.405**	**<0.001*** **
		Unmanaged	-0.045	0.051	-0.879	0.379
		Perennial	**-0.949**	**0.382**	**-2.487**	**0.013***
		Non-farmed % at 200 m radius	**0.091**	**0.032**	**2.846**	**0.004** **
		Biotic	-0.596	0.439	-1.356	0.175
		Unmanaged : Perennial	**0.404**	**0.034**	**12.032**	**<0.001*** **
		Unmanaged : Non-farmed % at 200 m radius	0.040	0.050	0.801	0.423
		Perennial : Non-farmed % at 200 m radius	**-0.127**	**0.017**	**-7.384**	**<0.001*** **
		Unmanaged : Biotic	**-0.126**	**0.047**	**-2.665**	**0.008** **
		Non-farmed % at 200 m radius : Biotic	0.041	0.024	1.710	0.087
300 m	66183	**(Intercept)**	**-1.351**	**0.307**	**-4.396**	**<0.001*** **
		Unmanaged	-0.039	0.051	-0.752	0.452
		Perennial	**-0.943**	**0.384**	**-2.455**	**0.014***
		Non-farmed % at 300 m radius	**0.121**	**0.033**	**3.642**	**<0.001*** **
		Biotic	-0.596	0.440	-1.355	0.175
		Unmanaged : Perennial	**0.396**	**0.034**	**11.795**	**<0.001*** **
		Unmanaged : Non-farmed % at 300 m radius	0.032	0.049	0.642	0.521
		Perennial : Non-farmed % at 300 m radius	**-0.151**	**0.017**	**-8.788**	**<0.001*** **
		Unmanaged : Biotic	**-0.125**	**0.047**	**-2.644**	**0.008** **
		Non-farmed % at 300 m radius : Biotic	0.040	0.024	1.648	0.099
400 m	66188	**(Intercept)**	**-1.350**	**0.308**	**-4.379**	**<0.001*** **
		Unmanaged	-0.042	0.051	-0.813	0.416
		Perennial	**-0.945**	**0.386**	**-2.450**	**0.014***
		Non-farmed % at 400 m radius	**0.120**	**0.033**	**3.618**	**<0.001*** **
		Biotic	-0.598	0.443	-1.351	0.177
		Unmanaged : Perennial	**0.401**	**0.034**	**11.936**	**<0.001*** **
		Unmanaged : Non-farmed % at 400 m radius	0.029	0.049	0.594	0.553
		Perennial : Non-farmed % at 400 m radius	**-0.143**	**0.017**	**-8.279**	**<0.001*** **
		Unmanaged : Biotic	**-0.124**	**0.047**	**-2.618**	**0.009** **
		Non-farmed % at 400 m radius : Biotic	**0.058**	**0.024**	**2.370**	**0.018***
500 m	66216	**(Intercept)**	**-1.345**	**0.307**	**-4.374**	**<0.001*** **
		Unmanaged	-0.048	0.051	-0.943	0.345
		Perennial	**-0.952**	**0.384**	**-2.479**	**0.013***
		Non-farmed % at 500 m radius	**0.096**	**0.033**	**2.878**	**0.004** **
		Biotic	-0.598	0.442	-1.352	0.176
		Unmanaged : Perennial	**0.408**	**0.034**	**12.177**	**<0.001*** **
		Unmanaged : Non-farmed % at 500 m radius	0.023	0.049	0.462	0.644
		Perennial : Non-farmed % at 500 m radius	**-0.111**	**0.017**	**-6.412**	**<0.001*** **
		Unmanaged : Biotic	**-0.125**	**0.047**	**-2.642**	**0.008** **
		Non-farmed % at 500 m radius : Biotic	**0.067**	**0.024**	**2.738**	**0.006** **

Significance codes: *** *P* < 0.001, ** *P* <0.01, * *P* <0.05. Statistically significant variables are indicated in bold

Chapter 3: Effects of plant functional traits on soil stability: intraspecific variability matters

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Invitation for resubmission at *Plant and Soil*

Abstract

Background and Aims: Soil stability is a key ecosystem function provided by agricultural landscapes. A multitude of influential factors such as soil texture and plant community structure have been suggested, but few studies compare the relative importance of these factors for soil stability in the field. In addition, studies on effects of plant traits on soil stability have ignored intraspecific trait variability (ITV) despite growing evidence of its importance for ecosystem functioning.

Methods: Using path model analysis, we quantified the effect of plant functional traits (PFTs), abiotic soil characteristics (soil texture) and vegetation characteristics on three soil stability measures in 30 field margins of an agriculture landscape of Korea, comparing models with and without ITV.

Results: Variance in soil stability was explained to varying degrees (from 81% for soil aggregate stability to 35% for soil shear vane strength). The three soil stability measures were mainly affected directly by root density, while PFTs and soil texture exerted indirect effects through root density and vegetation parameters, respectively. Including ITV improved model explained variance and goodness-of-fit in all cases.

Conclusion: The current study demonstrates that considering ITV is essential for uncovering the substantial effect of plant functional community composition on a key ecosystem function, soil stability.

Keywords: agricultural landscapes, community-weighted mean traits, intraspecific trait variability, plant functional traits, response and effect traits, root density, soil stability.

3.1 Introduction

Understanding the processes that drive the degradation of ecosystem functions in agricultural landscapes is of pivotal interest given ongoing land-use and climate change (Cardinale *et al.*, 2012). Although ecosystem functions are strongly affected by the direct impact of these abiotic drivers, it is also modulated by biotic factors (Loreau *et al.*, 2001). A number of studies has aimed at identifying the most important biotic drivers and it has been suggested that often the functional composition of ecological communities is more important for the maintenance of ecosystem functioning than species richness *per se* (Diaz *et al.*, 2006; Laughlin, 2014).

Different metrics of functional community composition can be measured in different ways. Recent studies suggest that community weighted means of functional traits (CWM), obtained by taking the mean trait value of a species weighted by its relative abundance in the focal community and then summed over all species (Garnier *et al.*, 2004), relate better to ecosystem functioning than functional diversity metrics (Fortunel *et al.*, 2009; Laughlin, 2011). Even though commonly applied (Garnier *et al.*, 2004; Díaz *et al.*, 2007) this metric has the problem that it ignores intraspecific trait variability. However, intraspecific variability can be large and is often not random but a result of adaptation or phenotypic plasticity of traits either along environmental gradients (Sandquist & Ehleringer, 1997), or a response to biotic interactions (Gross *et al.*, 2009; Albert *et al.*, 2011). Intraspecific trait variability, thus, can strongly influence the estimates of community trait composition (Jung *et al.*, 2014). Consequently, it has been strongly advocated to account for intraspecific variability when calculating CWMs (Albert *et al.*, 2010).

Here, we suggest studying community weighted means accounting for intraspecific trait variability, in order to better understand how different abiotic variables, vegetation characteristics and plant functional traits interact to influence an important ecosystem function: soil stability. Soil stability refers to the ecosystem function of resistance to disintegration when disturbed. Soil stability is critical for water infiltration, root growth, and resistance to water and wind erosion (Bronick & Lal, 2005; Gyssels *et al.*, 2005) and thus is a crucial soil property affecting soil sustainability and crop production (Letey, 1985). Soil stability can be measured in the field by several methods. The most common are: (1) Soil aggregate stability, which reflects how the soil aggregates react to precipitation, as the unstable aggregates tend to produce a slaked soil layer when it gets wet, which causes limitation in the infiltration rate, increasing the surface runoff and limiting the plant growth (Tisdall & Oades, 1982). (2) Soil penetration resistance, a composite soil property that is governed by more basic properties, including soil cohesion, soil compressibility and soil/metal friction (Dexter *et al.*, 2007). Penetration resistance correlates with several other important variables, such as root elongation rate (Taylor & Ratliff, 1969). (3) Soil shear vane strength, which measures the soil cohesiveness and resistance to shearing forces exerted by gravity, moving fluids and mechanical loads (Morgan, 2009). It reflects how the soil-root matrix produces a type of reinforced earth, which is much stronger than the soil or the roots separately and how this matrix can resist the environmental factors and human activities (Simon & Collison, 2001).

There are many factors that control soil stability via direct and indirect pathways. Particularly important are abiotic soil characteristics such as soil texture and clay content (Denef & Six, 2005; Chenu *et al.*, 2011), biotic vegetation characteristics such as species richness, vegetation cover and plant diversity (Pohl *et al.*, 2009; Pérès *et al.*, 2013), and biotic functional characteristics such as plant roots, soil fauna, and microorganisms (Gyssels *et al.*, 2005). In the following, we will shortly review the available literature on the interdependencies of these different factors and will summarize them in a conceptual path model reflecting a hypothesis on how abiotic and biotic factors interact and affect soil stability directly or indirectly (Fig. 3.1): Abiotic soil characteristics (e.g. soil texture with clay and silt percentages) influence soil stability directly. For example, fine soil particles (clay and silt) tend to increase, while coarse particles (sand and gravel) decrease soil stability (Tisdall & Oades, 1982; Nearing *et al.*, 1991). They also influence vegetation characteristics (e.g. vegetation cover, species richness and root density) and functional characteristics of plant communities, i.e. plant functional traits (PFTs) such as root/shoot ratio, root length and root horizontal width (Lane *et al.*, 1998). Biotic vegetation characteristics also directly influence soil stability: Both above ground vegetation characteristics such as higher species richness, plant cover, and species diversity (Pohl *et al.*, 2012; Pérès *et al.*, 2013), as well as below ground vegetation characteristics, such as higher root length, root density, and root length density (Pohl *et al.*, 2009; Hu *et al.*, 2013) increase soil stability. The effect of vegetation characteristics on soil stability is due to multiple processes. First, plant roots forming a dense root network bind soil particles via root excretions (Traore *et al.*, 2000; Gyssels *et al.*, 2005). Secondly, a dense above ground vegetation protects the soil surface from wind and rain drops (Gray & Sortir, 1996). Thirdly, a dense vegetation and root network enhances infiltration rates and reduces runoff (Tisdall & Oades, 1982). Plant cover and species diversity impact not only soil stability but also species assembly in communities and thus the functional composition of communities (Petchey & Gaston, 2002). In return, it has been shown that vegetation characteristics and root density depend strongly on the functional composition of communities (Reich *et al.*, 2012). Finally, as argued before, species functional traits do not only respond to local abiotic and biotic characteristics but they also play an important role in ecosystem functions. For soil stability it has been shown that root length, root diameter and root horizontal width are important determinants (Gyssels *et al.*, 2005; Pohl *et al.*, 2012).

The aim of this paper is to integrate vegetation characteristics and functional traits into a model of abiotic soil characteristic effects on soil stability, towards an improved understanding of ecosystem functioning. For this purpose we measured soil stability via soil aggregate stability, soil penetration resistance and soil shear vane strength. First, we test how well our conceptual model (outlined above and visualized in Fig. 3.1) fits data from field margins in an agriculture landscape in Korea and how important intraspecific variability is for this fit. Second, we investigate the importance of PFTs in comparison to the influence of abiotic soil characteristics and biotic vegetation characteristics for soil stability. Finally, we ask whether the identified functional effect traits are at the same time important functional response traits. In other words, are the traits that determine the effect on ecosystem functioning the same as those that determine the response of organisms to abiotic conditions (Lavorel & Garnier, 2002)?

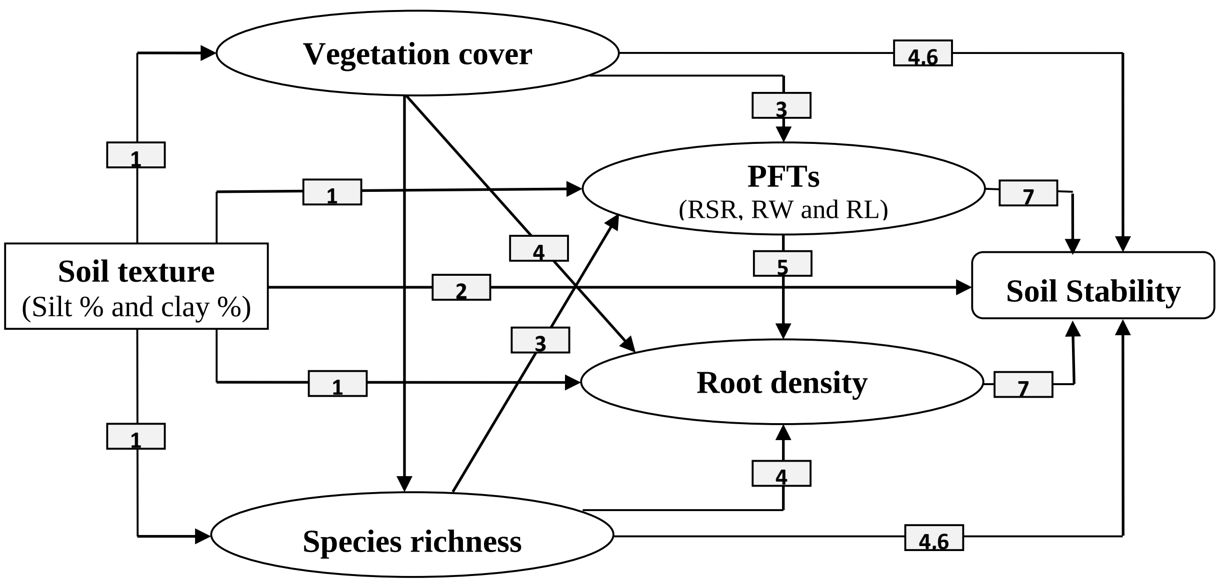

Fig. 3.1. A conceptual path model for effects of the abiotic soil characteristics (soil texture "silt % and clay %"), vegetation characteristics (vegetation cover, species richness and root density) and PFTs (RSR = root/shoot ratio, RL = root length and RW = root horizontal width) on three soil stability measures (Soil aggregate stability, soil penetration resistance and soil shear vane strength). Numbers on arrows indicate previous studies that support the path. 1. Lane *et al.* (1998), 2. Denef and Six (2005), 3. Petchey and Gaston (2002), 4. Pohl *et al.* (2009), 5. Reich *et al.* (2012), 6. Pérès *et al.* (2013)and 7. Gyssels *et al.* (2005).

3.2 Materials and methods

3.2.1 <u>Study site and experimental design</u>

The study was conducted in the Haean-myun catchment in South Korea, which is located in the watershed of Soyang Lake close to the Demilitarized Zone (DMZ; 128°05' to 128°11' E, 38°13' to 38°20' N; Fig. 3.2). Elevation in the study site varies from 500 to 750 m a.s.l. The mean annual air temperature is 10.5 ºC, mean monthly temperature varies between -10 ºC in January and 27 ºC in August (1999 - 2012).

The average precipitation is 1,500 mm, with 70% of the rain falling during the summer monsoon from June to August (Berger *et al.*, 2013). The area is subjected to very heavy rains during the monsoon season, which causes severe damages to the soil, and thus soil stability is a very important ecosystem function.

Over the whole catchment, 30 plots of 1 m^2 were randomly chosen. In each plot, we estimated (1) vegetation characteristics, (2) plant functional traits of 10 selected species, (3) soil characteristics (excluding soil stability) and (4) measures of soil stability.

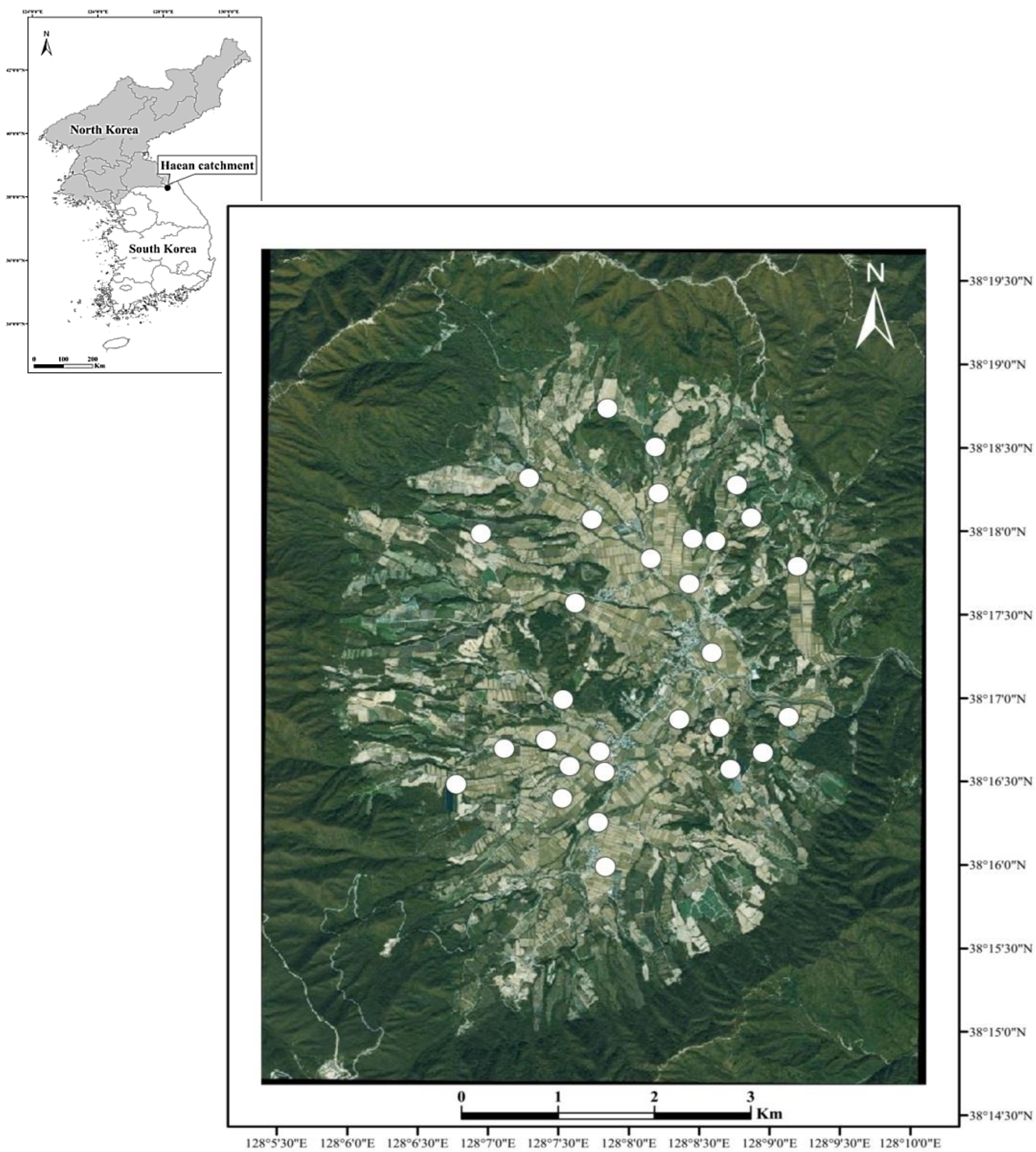

Fig. 3.2. The 30 sampling plots for the plant functional traits in Haean-myun catchment.

(1) Vegetation characteristics

In each plot, we estimated three different variables describing the vegetation characteristics: vegetation cover (i.e. the percentage of ground covered by vegetation), species richness (i.e. the number of observed species) and root density (estimated as percentage using a 30 cm x 30 cm metallic frame placed on the soil profile, following (Eckelmann, 2006).

(2) Plant functional trait measurement and analyses

We measured above- and belowground plant functional traits (PFTs) for 15 individuals of the 10 most representative species in the study site (Table 3.1). The 10 most representative species were chosen based on their abundance in an earlier intensive botanical survey we conducted at the study site (Chapter 2). To account for the community-level intraspecific variability of traits, we collected individuals in the plots, with a maximum of 3 individuals per species per plot. Depending on the distribution of the species, between 0 and 3 individuals of each species were collected in each plot. Following this sampling design we finally had trait information for an average of 51 % of the vegetation cover in the plots (min = 30% and max = 75%).

We collected the above- and belowground biomass of the 150 studied individuals. We measured plant height (Cornelissen *et al.*, 2003) and leaf size (Cornelissen *et al.*, 2003) for the aboveground compartment of each individual. We washed, dried, weighted and scanned the roots of each individual in order to measure root horizontal width (Cornelissen *et al.*, 2003; Lobet *et al.*, 2011), root length and diameter (Lobet *et al.*, 2011), root dry mass (Cornelissen *et al.*, 2003), specific root length (SRL), which is the root length divided by the root dry mass (Cornelissen *et al.*, 2003), and root/shoot ratio (Monk, 1966).

We then up-scaled functional properties to the community level using community weighted means for each of the PFTs (Garnier *et al.*, 2007; Violle *et al.*, 2007; Lavorel *et al.*, 2008). In order to investigate the importance of intraspecific trait variability we used two different CWM estimates, one that neglects intraspecific variability ($CWM_{species}$) and one that integrates it at the level of each local community (CWM_j). To account for intraspecific variability, we calculated the CWM_j within each plot based on the locally observed mean species trait value and the species' relative cover:

$$CWM_j = \sum_{i=1}^{n} p_{ij} * trait_{ij}$$

where p_{ij} is the relative cover % of species (i) in the community plot (j) and $trait_{ij}$ is the mean trait value of species (i) in the community plot (j). To calculate $CWM_{species}$ we used the overall species mean trait value instead of the locally observed mean species trait value.

Table 3.1. Above and below ground characteristics of the ten plant species studied in Haean-myun catchment.

Name	Family	Height (cm)	Root / shoot ratio	Root length (cm)	Root diameter (cm)	Root horizontal width (cm)	Specific root length (cm/g)	Leaf size (cm^2)
Artemisia princeps Pamp.	Asteraceae	88.03 (11.80)	0.24 (0.07)	20.55 (5.41)	0.24 (0.03)	18.25 (1.98)	14.03 (7.70)	75.28 (28.72)
Chelidonium majus var. *asiaticum* (Hara) Ohwi	Papaveraceae	83.07 (15.97)	0.12 (0.03)	19.41 (5.90)	0.23 (0.05)	10.77 (4.96)	13.38 (12.31)	99.83 (37.56)
Conyza canadensis (L.) Cronquist	Asteraceae	69.07 (11.25)	0.22 (0.05)	18.46 (3.60)	0.15 (0.03)	14.79 (5.72)	8.19 (4.99)	22.22 (4.65)
Equisetum arvense L.	Equisetaceae	30.27 (9.45)	0.38 (0.13)	22.12 (7.33)	0.17 (0.03)	3.44 (3.39)	89.07 (61.27)	2.28 (0.69)
Erigeron strigosus Muhl.	Asteraceae	82.53 (14.52)	0.26 (0.11)	15.11 (4.77)	0.04 (0.03)	13.87 (4.20)	15.73 (12.54)	24.68 (14.81)
Humulus japonicus Sieboid & Zucc.	Cannabaceae	88.00 (9.77)	0.07 (0.03)	18.57 (7.29)	0.04 (0.01)	4.19 (2.56)	120.52 (87.10)	108.40 (49.98)
Oenothera biennis L.	Onagraceae	81.07 (17.51)	0.19 (0.0)	28.55 (9.31)	0.33 (0.11)	18.25 (8.36)	6.85 (5.60)	39.24 (11.87)
Persicaria vulgaris Webb & Moq.	Polygonaceae	38.60 (18.02)	0.14 (0.06)	13.00 (4.12)	0.14 (0.19)	7.39 (4.51)	49.33 (31.65)	27.98 (12.99)
Phragmites japonica Steud.	Poaceae	77.8 (25.61)	0.48 (0.25)	24.25 (10.43)	0.11 (0.04)	13.06 (4.56)	19.12 (13.51)	52.11 (26.88)
Rorippa palustris (Leyss.) Besser	Brassicaceae	50.47 (13.8)	0.16 (0.08)	15.55 (5.32)	0.08 (0.02)	7.89 (4.29)	24.63 (13.57)	25.91 (17.12)

Values are means with standard deviation in parentheses.

(3) Soil characteristic measurements and analyses (excluding stability):

In each plot, we estimated five different soil variables: Bulk density, water content, wettability, clay % (i.e. percentage of clay), and silt % (i.e. percentage of silt). We randomly sampled 30 cm deep soil profiles (from 0 to 30 cm) at each plot. For the bulk density, we took three samples from the soil profile using soil rings with 2.8 cm diameter and 1 cm height. Soil rings were weighted, oven-dried for 24 hours at 105°C and finally weighed again (Avnimelech *et al.*, 2001). Bulk density was calculated using the following equation:

$$\text{Bulk density (g/cm}^3\text{)} = \text{dry sample mass / total sample volume}$$

The soil water content was calculated as the difference between the ring mass before and after drying.

Soil wettability was assessed via the “water drop penetration time” (WDPT) (Letey, 1969). Droplets of distilled water were placed onto the surface of the soil sample and the time for their complete infiltration was recorded. Measurements were replicated 10 times for each sample, and then the mean value was used for our analysis.

Soil texture was expressed as clay % and silt %, following the standard sieve-pipette method procedures as described by Gee and Bauder (1986); soil samples were first dispersed into individual primary particles using hydrogen peroxide (H_2O_2) and sodium hexametaphosphate 4%, then the soil slurry was sieved through 0.63 mm, 0.2 mm and 0.063 mm sieves to separate coarse, medium and fine sand fractions. The remaining suspension, containing coarse, medium and fine silt and clay, was then transferred to a 1 liter cylinder and after stirring a sample was taken using a 50 ml pipet at different time intervals depending on the temperature, to sample the fine, medium and coarse silt and clay. After drying and weighting the samples, % pipetted fraction was calculated as:

% pipetted fraction = (mass of the oven dry fraction / mass of the original sample) x 100

In addition, we used the soil profiles to estimate root density (a variable describing vegetation characteristics, see above).

(4) Soil stability measurements

The plot specific soil cores were also used to estimate variables of soil stability. We considered three different and commonly used variables: soil aggregate stability, penetration resistance and soil shear vane strength. We used the modified wet sieving method by (Haynes, 1993) to measure soil aggregate stability, based on one surface soil sample per plot. In this method 100g of the air-dried 24mm soil aggregates were transferred to the uppermost of a set of five sieves with apertures ranging from 0.05 to 2 mm. Then the sieves' set were transferred to a water-path where the oscillation rate was 2.5 cycles per minute and the amplitude of the sieving action was 3.5 cm for 15 min. Then the sieves were oven dried at 105ºC for 24 hours and the remaining aggregates at each sieve were weighted and the mean weight diameter (MWD) was calculated as follows:

$$\text{MWD} = \sum w_i * x_i$$

where i corresponds to each fraction collected, w_i is the dry mass of the fraction collected relative to the total soil used and x_i is the mean diameter of the fraction collected.

In each of the 30 plots, we measured soil penetration resistance (kg/cm^2) using a EW-99039-00 pocket penetrometer (Cole-Parmer Cole-Parmer Instrument Company, Vernon Hills, IL., USA). Measurements of penetration resistance were replicated three times for each plot and the average value of them was included in the models.

For measuring soil shear vane strength (kPa), we used a shear vane with a height of 80 mm and a diameter of 40 mm with three measures per plot. Shear strength was calculated using the following equation:

$$\tau_f = \frac{T}{2\pi\, r_v^2 \left(\left(\frac{2}{3}\right) r_v + h \right)}$$

where τ_f is the shear strength of the soil, T is the maximum torque at failure, h is the height of the vane and r_v is the diameter of the vane (Richards, 1988). Three replicate measurements were made at each plot and the average value was used in the models.

3.2.2 Statistical Analyses

The aim of our study was to evaluate our conceptual path model on the influence of vegetation characteristics, soil characteristics and PFTs on soil stability that we developed in the introduction (Fig. 3.1) with our data. Towards this aim path analyses were performed independently for the three measures of soil stability.

In a first step, owing to the demanding field protocol of measuring intraspecific trait variability, which resulted in a limited sample size, we reduced the number of variables measured to describe vegetation characteristics, soil characteristics and PFTs. As suggested by Wilson and Nussey (2010), variable selection was based on a redundancy analysis (RDA), which allowed us to choose those variables and traits that showed a significant relation to soil stability. We performed this independent pre-variable selection in order to obtain a common set of variables for all three soil stability measures and thus for all three independent path analyses.

In a second step, we fitted the conceptual path model with all remaining variables based on a Partial Least Squares Path Modeling (PLS-PM) approach. Model evaluation of PLS-PMs was based on the R^2 coefficient for the soil stability measure and the overall model goodness-of-fit (GoF) index. All statistical analyses were done using R, version 3.1.0 (R Development Core Team, 2014), with package *PLSPM* (Sanchez *et al.*, 2013) for the path analysis, the RDA was done using R package *vegan* (Oksanen *et al.*, 2014).

3.3 Results

We found large intraspecific trait variability within the measured traits (Fig. 3.S1). Species mean values ranged from 0.06 to 0.47 for root/shoot ratio (Fig. 3.S1a), from 13.00 to 28.55 cm for root length (Fig. 3.S1b), and from 3.44 to 18.25 cm for root horizontal width (Fig. 3.S1c).

According to the RDA (Table 3.2), the vegetation variables that best describe soil stability were “vegetation cover percentage, species richness and root density”. For the soil characteristics, the soil texture variables “silt and clay percentages” were most important and for the PFTs “root/shoot ratio, root horizontal width and root length”. We kept these variables in the following PLS-PM approaches, which we describe independently for the three variables of soil stability.

We fitted of our conceptual path model to data either by ignoring intraspecific trait variability (using $CWM_{species}$ as metrics for the PFTs) or by accounting for it at the scale of the communities (using CWM_j as metrics for the PFTs).

Ignoring intraspecific trait variability resulted in lower quality performance of our path models; the explained variance was 79%, 49% and 35% for aggregate stability, penetration resistance and shear vane strength, respectively, and goodness-of-fit was 0.45, 0.41 and 0.38 (see Table 3.S1; Figs. 3.S2, 3.S3). Direct and indirect effects of PFTs on soil stability were negligible (with standardized path coefficients, spc, 0.16, 0.09 and -.03 for the three stability measures). We therefore decided only to present the results of the models accounting for intraspecific variability in more detail.

3.3.1 Soil aggregate stability (models accounting for intraspecific variability)

Our conceptual path model explained 81% of the variance of soil aggregate stability with a goodness-of-fit index of 0.58 (Fig. 3.3a). Root density and vegetation cover were the most important factors that directly affected soil aggregate stability (with standardized path coefficients, spc, of 0.55 and 0.26 respectively), while the indirect effects of soil texture and the PFTs on soil aggregate stability resulted in the highest total effects (with spc equal to 0.66 and 0.50 respectively, Table 3.S2; Fig. 3.4a). The high total effects of soil texture resulted from the strong direct effects of soil texture on PFTs and vegetation cover (and partly on species richness, which had a moderate effect on soil aggregate stability), while the high total effects of PFTs resulted from their strong link to root density which itself had a strong influence on soil aggregate stability. Moreover, PFTs were significantly affected by soil texture and species richness.

The crossloading effects that allow differentiating between the different PFTs (i.e. root/shoot ratio, root length and root horizontal width) (Fig. 3.5a) showed that the root/shoot ratio has the strongest effect on soil aggregated stability (spc = 0.72) followed by root length (spc = 0.54) and root horizontal width (spc=0.52, Fig. 3.5a). The silt and clay percentages had similar effects on soil aggregated stability (with spc equal to 0.65 and 0.60 respectively).

Table 3.2. Redundancy analysis (RDA) results between the three stability measures and the vegetation, soil parameters and plant functional traits (PFTs).

Vegetation parameters	RDA 1 (46.2%)	RDA 2 (1.2%)
Vegetation Cover	**-0.453**	-0.802
Species richness	**-0.680**	-0.243
Root density	**-0.960**	0.278
Soil parameters	RDA 1 (42.9%)	RDA 2 (1.4%)
Bulk density	-0.399	-0.322
Water content	-0.225	-0.691
Wettability	-0.332	-0.595
Clay %	**-0.794**	0.427
Silt %	**-0.857**	0.295
Plant functional traits	RDA 1 (49.5%)	RDA 2 (3.9%)
Plant height	**-0.540**	0.180
Root/shoot ratio	**-0.790**	-0.463
Root length	**-0.544**	0.265
Root diameter	0.225	-0.598
Root horizontal width	**-0.372**	-0.656
Specific root length	-0.087	0.575
Leaf size	0.110	0.452

3.3.2 Penetration resistance (models accounting for intraspecific variability)

For the soil penetration resistance, our conceptual path model explained 50% of the variance with a goodness-of-fit index of 0.54 (Fig. 3.3b). Root density and soil texture were the most important factors that directly affected soil aggregate stability (with standardized path coefficients, spc, of 0.58 and 0.44 respectively), while PFTs showed the strongest indirect effect on penetration resistance (with spc equal to 0.30, Table 3.S2; Fig. 3.4b). These strong indirect effects of PFTs resulted from their strong link to root density which itself had a strong influence on soil penetration resistance. As in the soil aggregate stability model, PFTs were significantly affected by soil texture and species richness.

The crossloading effects showed a slightly different order of relative importance of the different PFTs (Fig. 3.5b) than in the soil aggregate stability model: For soil penetration resistance, root length (and not root/shoot ration) was most important (spc = 0.51) followed by root/shoot ration (spc = 0.48) and root horizontal width (spc = 0.20, Fig. 3.5b). The silt and clay percentages showed the same trends as in the soil aggregate stability model (spc = 0.54 and 0.53 respectively).

3.3.3 Soil shear vane strength (models accounting for intraspecific variability)

In the soil shear vane strength model, 35% of the variance was explained, with a goodness-of-fit index of 0.52 (Fig. 3.3c). Root density was the most important factor that directly affected soil shear vane strength (spc = 0.54), while the indirect effects of soil texture and PFTs on shear vane strength had the highest total indirect effects (spc = 0.52 and spc = 0.22, respectively, Table 3.S2; Fig. 3.4c). Soil texture had a strong direct effect on PFTs and species richness. PFTs showed a strong relation to root density which itself had a strong influence on shear vane strength. As before, PFTs were significantly affected by soil texture and species richness.

The crossloading effects were comparable to those in the penetration resistance path model (Fig. 5c), as both the root/shoot ratio and root length were most important (spc = 0.43 and 0.40 respectively), while the root horizontal was much less important (spc = 0.10). As before, silt and clay percentages were equally important (spc = 0.47 and 0.40 respectively).

Overall, we found that ignoring intraspecific trait variability resulted in lower fit for our conceptual model to the data. Accounting for intraspecific variability, the three components of soil stability were either moderately (soil shear vane strength, soil penetration resistance) or well (soil aggregate stability) explained by our conceptual path model. In all three analyses, root density had the strongest direct effect on soil stability. Accounting in addition for indirect effects, we could show that PFTs had a similarly strong influence, which was mostly mediated by root density. The most important PFTs were root length and the root/shoot ratio. PFTs themselves were strongly affected by species richness and soil texture.

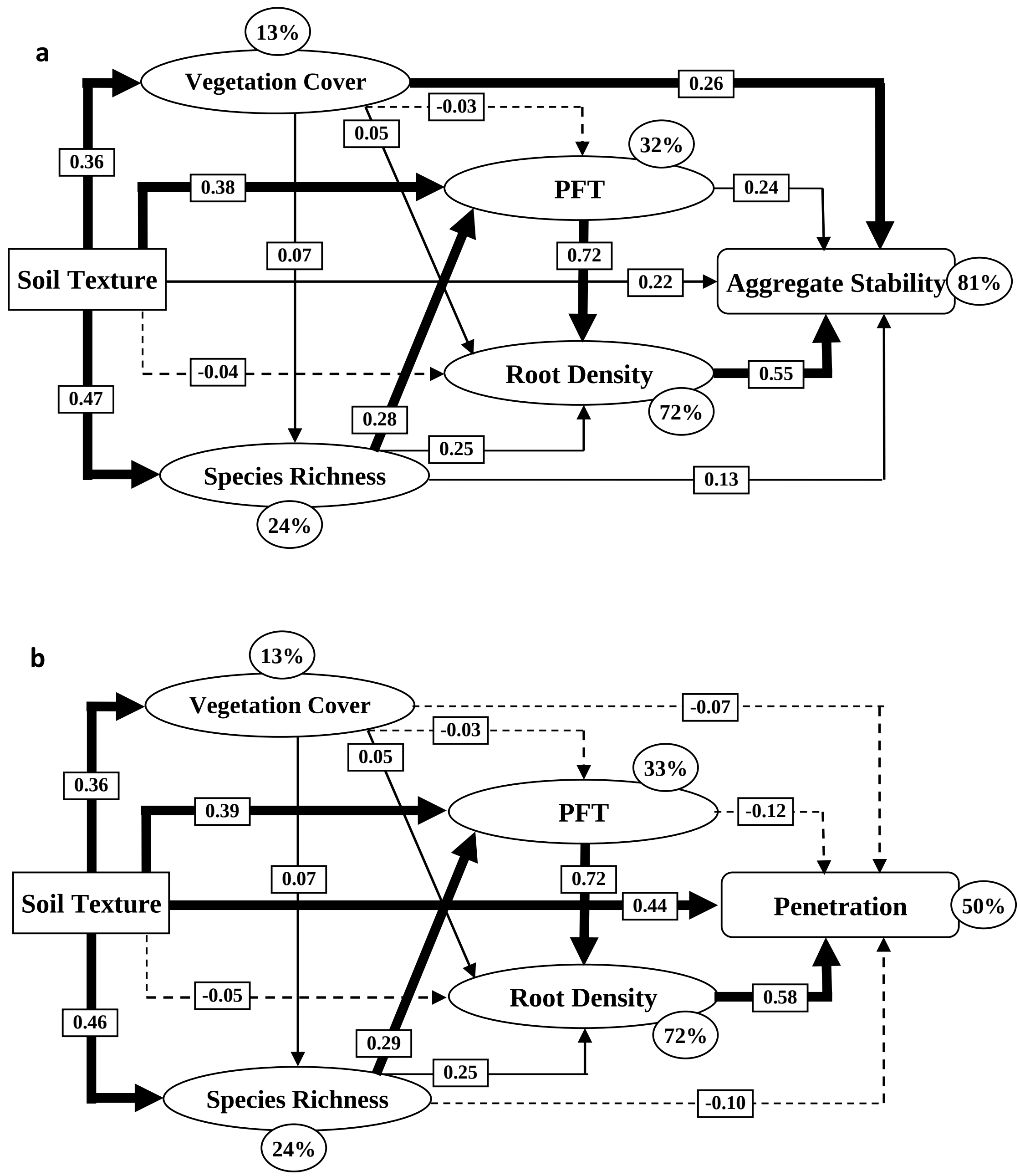

Fig. 3.3. The path models outputs for the effects of the soil texture "silt % and clay %", vegetation cover, species richness, root density and PFTs "root/shoot ratio, root length and root horizontal width" with accounting for the intraspecific trait variability, on three soil stability measures. (a) soil aggregate stability (b) penetration resistance and (c) soil shear vane strength. Numbers on arrows are standardized path coefficients. Solid arrows are positive and dashed are negative, bold arrows indicate significant standardized paths (P < 0.05); thin arrows indicate non-significant path coefficient ($P > 0.05$). Percentages close to the boxes indicate the variance explained by the model (R^2). The goodness-of-fit indices for the models are 0.58 for (a), 0.54 for (b) and 0.52 for (c).

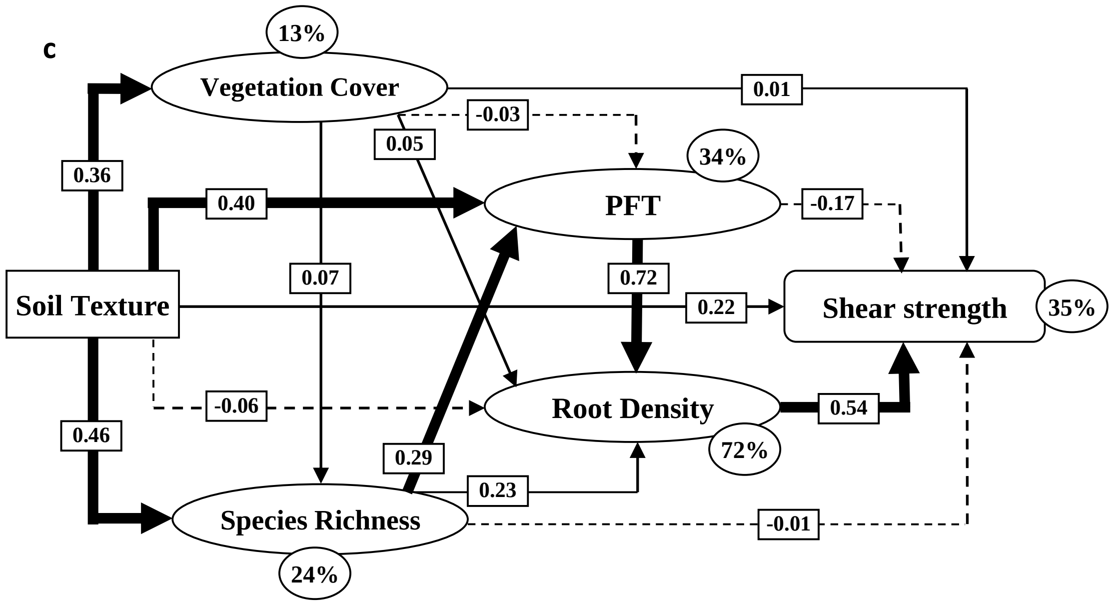

Fig. 3.3 (cont.). The path models outputs for the effects of the soil texture "silt % and clay %", vegetation cover, species richness, root density and PFTs "root/shoot ratio, root length and root horizontal width" with accounting for the intraspecific trait variability, on three soil stability measures. (a) soil aggregate stability (b) penetration resistance and (c) soil shear vane strength. Numbers on arrows are standardized path coefficients. Solid arrows are positive and dashed are negative, bold arrows indicate significant standardized paths (P < 0.05); thin arrows indicate non-significant path coefficient (P > 0.05). Percentages close to the boxes indicate the variance explained by the model (R^2). The goodness-of-fit indices for the models are 0.58 for (a), 0.54 for (b) and 0.52 for (c).

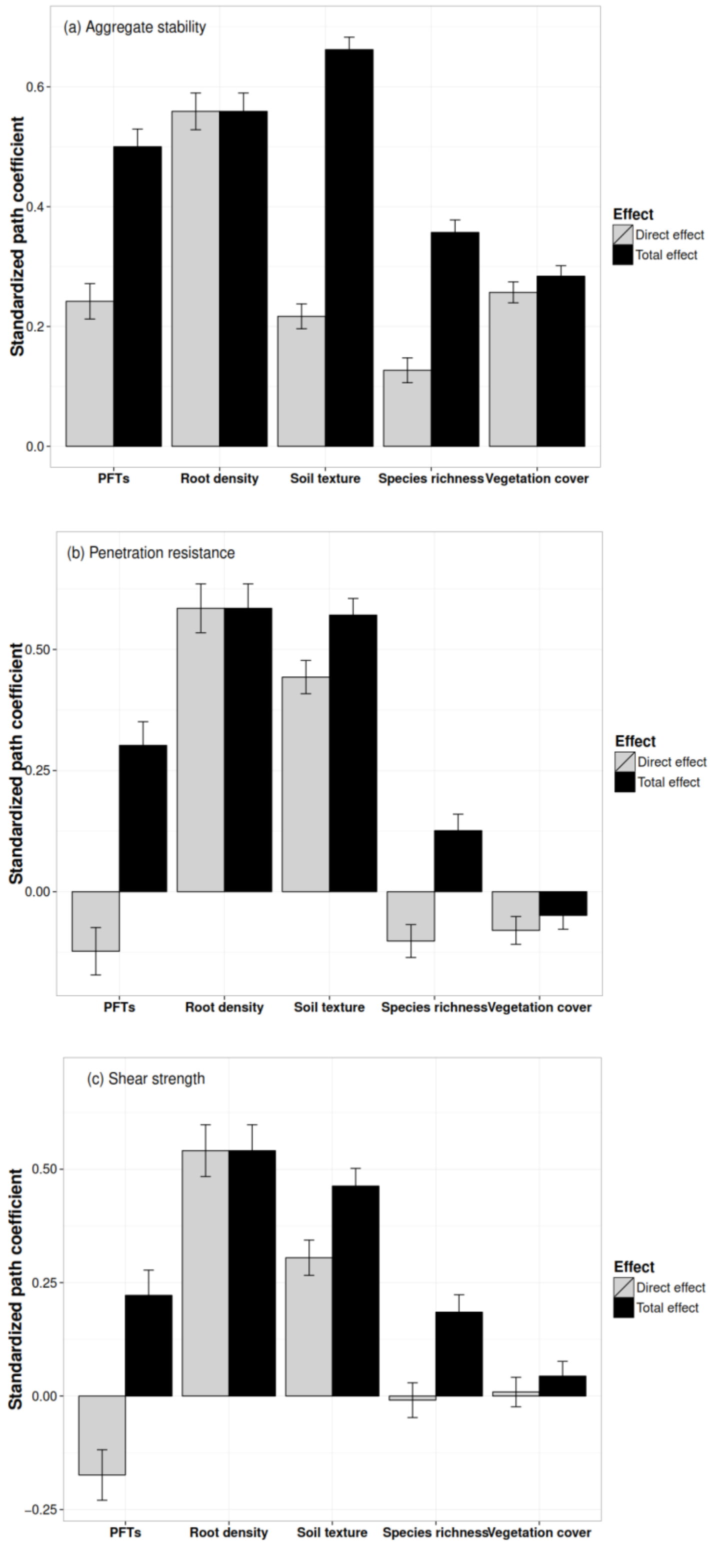

Fig. 3.4. The standardized path coefficient for direct and indirect effects of PFTs "root/shoot ratio, root length and root horizontal width", root density, soil texture "silt % and clay %", species richness and vegetation cover on (a) soil aggregate stability, (b) soil penetration resistance and (c) soil shear strength.

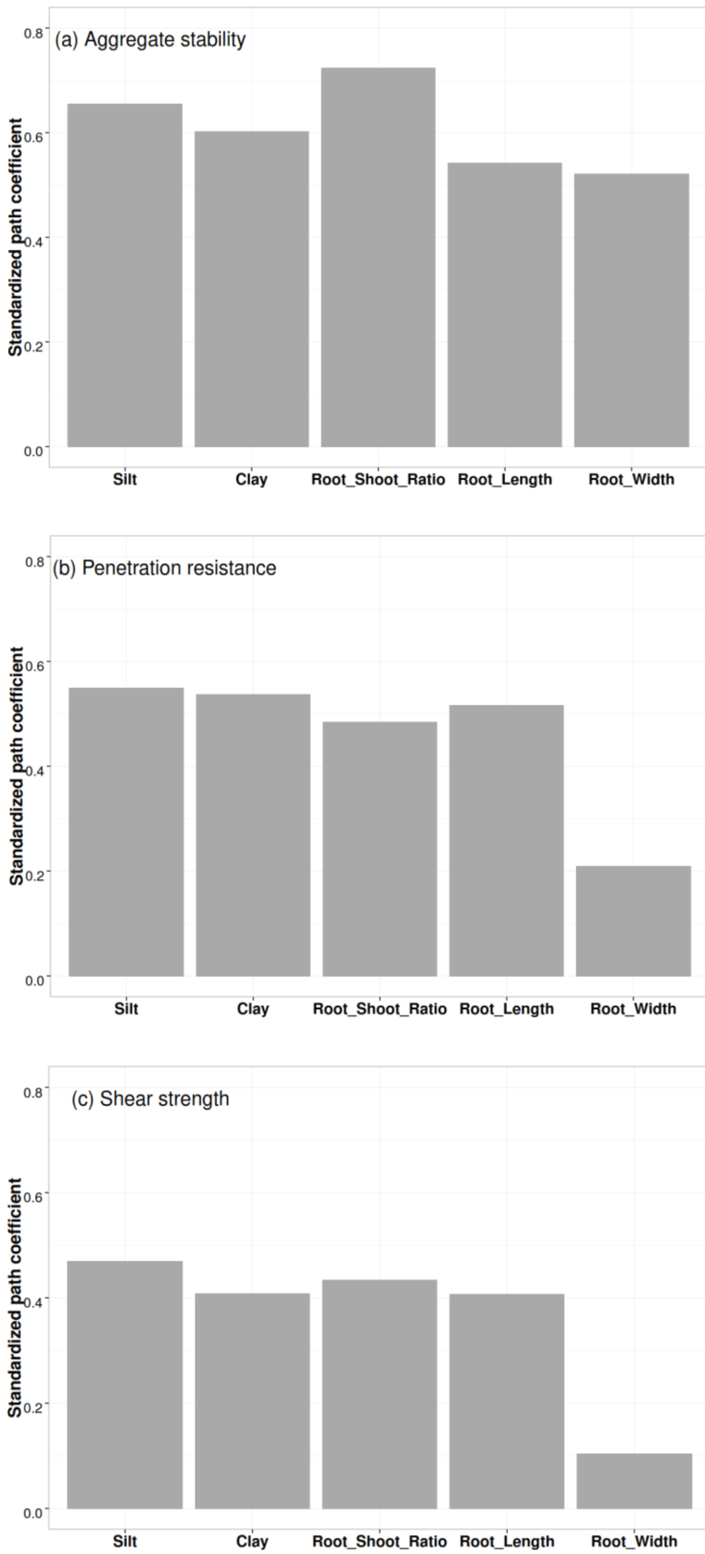

Fig. 3.5. The path model crossloadings effect of the soil texture "silt and clay contents" and PFTs "root/shoot ratio, root length and root horizontal width" on (a) soil aggregate stability, (b) soil penetration resistance and (c) soil shear strength.

3.4 Discussion:

Our study is one of the few to investigate the combined influence of plant functional traits (PFTs), vegetation characteristics and abiotic soil characteristics on ecosystem functioning in the field. We built a conceptual path model to disentangle the different abiotic and biotic drivers of soil stability as one of the important ecosystem functions impacting erosion control and nutrient supply in agriculture landscapes. We confronted this model with data collected in field margins in South Korea. Results highlight the important effect of the functional composition of communities on soil stability. Notably, this effect could only be seen when considering intraspecific variability in PFTs.

3.4.1 Explained variation in soil stability

Our conceptual model hypothesizes that soil stability is not only strongly influenced by abiotic variables (e.g. soil structure) and vegetation structure (e.g. cover, species richness) but also by the functional composition of plant communities. Overall, our data from South Korean field margins support this hypothesis.

When intraspecific trait variability was considered, the conceptual model explained moderate to large parts of the variation in the three considered measures of soil stability. Aggregated stability was best explained (81%) followed by penetration (50%) and shear strength (35%). In comparison, goodness-of-fit values were not very high (0.52-0.58), a result that is due to the relative low sample size resulting from the considerable practical challenge posed by the indispensability of accounting for intraspecific variability in trait compositions.

The three measures of soil stability quantify different facets of soil stability: Aggregate stability has a strong influence on infiltration rate and surface runoff (Gyssels *et al.*, 2005); penetration resistance strongly influences root elongation rates (Dexter *et al.*, 2007), and is further related to retention, erosion, crusting and nutrient cycling (Bronick & Lal, 2005; Chapman *et al.*, 2012); finally, soil shear strength influences the resistance of the soil-root matrix to disturbances (Simon & Collison, 2001), erosion (Morgan 1996), and crushing (Gyssels *et al.*, 2005). While the amount of variation explained by our models differed across these three facets of soil stability, the models were largely congruent in the attribution of relative importance to soil texture, root density, and, notably, the role of intraspecific variability in PFTs, emphasizing the robustness of our results.

3.4.2 Importance of plant functional traits and intraspecific variability

One of our most striking results is that fitting the conceptual model with average trait data (i.e. ignoring intraspecific trait variability) led to poor model performance. Especially, the effect of functional plant community composition on the different components of soil stability was strongly underestimated when ignoring intraspecific variability. In addition we found that even though species significantly differ in their mean trait values, intraspecific trait variation is large and trait distributions of different species overlap (see supplementary material, Fig. 3.S1). Together these results imply that soil stability is significantly influenced by functional plasticity of plants.

The abiotic variable soil texture was the most important variable in our model. The fine particles of the soil texture (clay and silt) improve soil stability (Tisdall & Oades, 1982; Nearing *et al.*, 1991; Chenu *et al.*, 2011). It has been currently suggested that this positive effect is rather due to the electrostatic bonds or physical forces (Denef & Six, 2005; Arvidsson & Keller, 2011), than due to organic cementing agents (Six *et al.*, 2000). Functional community composition and root density had very strong impacts as well. Root/shoot ratio, root length and root horizontal width influenced all components of soil stability strongly and mostly via their impacts on root density. The effect of root/shoot ratio, root length or root horizontal width is mediated via root density due to its role in (1) microbial community compositions in the rhizosphere which in turn supports soil stability (Gyssels & Poesen, 2003), (2) in reducing soil porosity (Pohl *et al.*, 2009; Graf & Frei, 2013; Pérès *et al.*, 2013), and (3) binding soil particles together via root exudates and mucilage (Pojasok & Kay, 1990; Traore *et al.*, 2000; Eisenhauer *et al.*, 2010).
Interestingly, the effect of PFTs on soil stability via root density is much more important than the effects of species richness and partly vegetation cover, a result that is in concordance with recent literature (Graf & Frei, 2013; Pérès *et al.*, 2013). Species richness did not directly affect soil stability at all but affected root density and PFTs. The impact of vegetation cover was overall small. Our results highlight, the importance of not only abiotic but also biotic variables for soil stability. The most important biotic variables are strongly related to ecosystem functioning.

To our knowledge, this is the first field study to demonstrate the key role of plant functional traits in soil stability, while accounting for intraspecific trait variability. Soil stability of field margins is of particular relevance for agricultural landscapes subjected to extreme heavy rains during the monsoon season, as it contributes to the control of soil erosion and nutrient cycling. Our results further corroborate the notion that ecosystem functions (e.g. soil stability) are related to the functional composition of the community rather than species diversity *per se* (Díaz & Cabido, 2001).

3.4.3 Effect vs. response traits

In our analyses we first selected effect traits that related well to soil stability. The integration of these effect traits into our conceptual model allowed us then to evaluate if the same traits well described responses to abiotic conditions. Results showed a strong influence of soil texture on PFTs. Consequently we can conclude that root/shoot ratio, root length and root horizontal width, are at the same time important response and effect traits.

Our results suggest that understanding the response of plant communities to abiotic conditions benefits from accounting for plant phenotypic plasticity. High plant phenotypic plasticity in response and effect traits renders the challenge of managing field margins more difficult and simpler; more difficult, because management is difficult to optimize when targeting species based on their mean traits is not likely to work, and simpler, because management will be robust when several target species can provide the same required effect traits.

3.4.4 Conclusion

Our study demonstrates the important role of intraspecific trait variability not only in responses of plant communities to changing conditions but also in their effect on key ecosystem functions. Results corroborate for an important specific example (soil stability in agricultural landscapes) earlier findings suggesting that the functional trait composition of communities can be much more important for ecosystem functioning than vegetation cover or species richness. These findings have important implications for managing field margins in order to improve soil stability as communities should not only be enriched by species with favorable root traits but it should also be considered that species show important plasticity in their root traits.

3.5 Acknowledgement

This work is part of the International Research Training Group ‘‘Complex TERRain and ECOlogical Heterogeneity” (TERRECO) (GRK 1565/1) funded by the German Research Foundation (DFG). We thank Sebastian Arnhold, Mareike Ließ, Marianne Ruidisch and Iris Schmiedinger for supporting us in the field and the lab work, Bernd Huwe for his comments and suggestions on our field protocol and soil analyses and John Tenhunen for his comments and coordination of the TERRECO fieldwork.

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3.7 Supplementary Materials

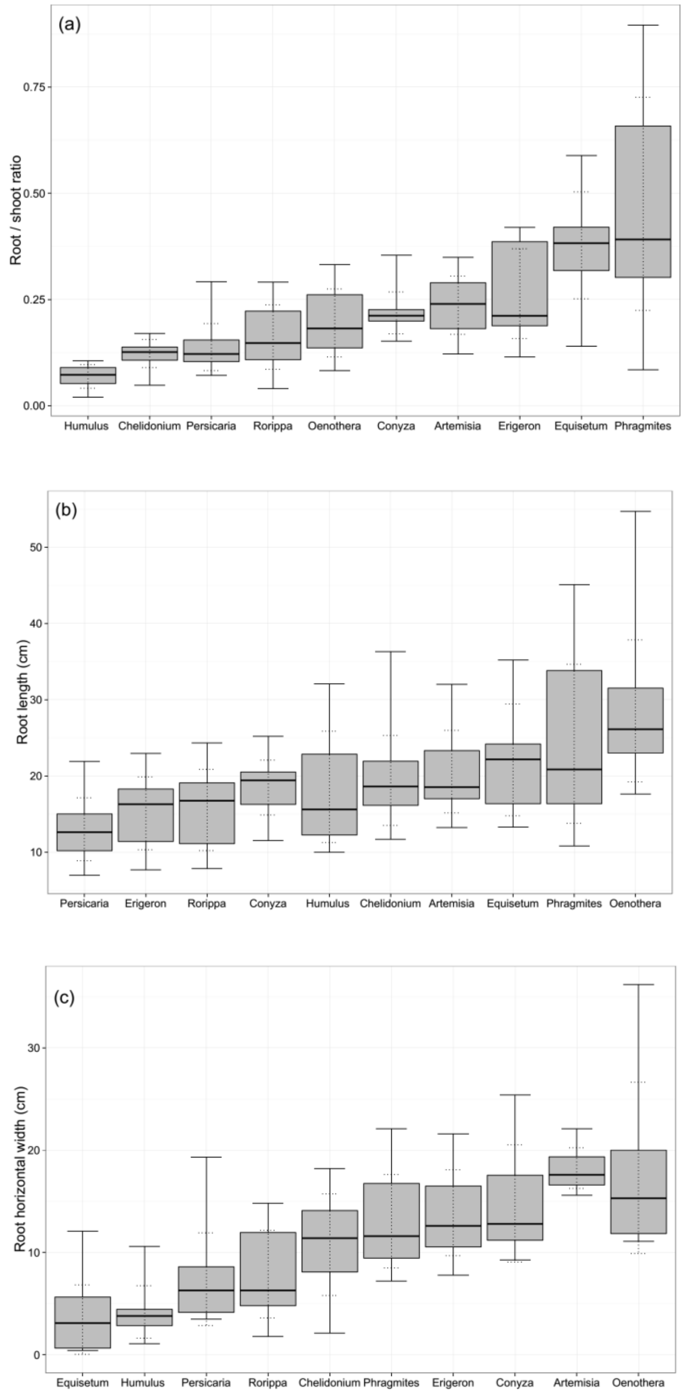

Fig. 3.S1. Boxplots showing the intraspecific functional variability for (a) root/shoot ratio, (b) root length and (c) root horizontal width across the ten studied species. It represents (i) the first and third quartile (extent of the boxes), (ii) the median value (bold black dash), (iii) the maximum and minimum values of the traits (black whiskers) and (iv) the standard deviation of the mean (dotted whiskers). For each trait, results are presented by species ordered by increasing mean trait values.

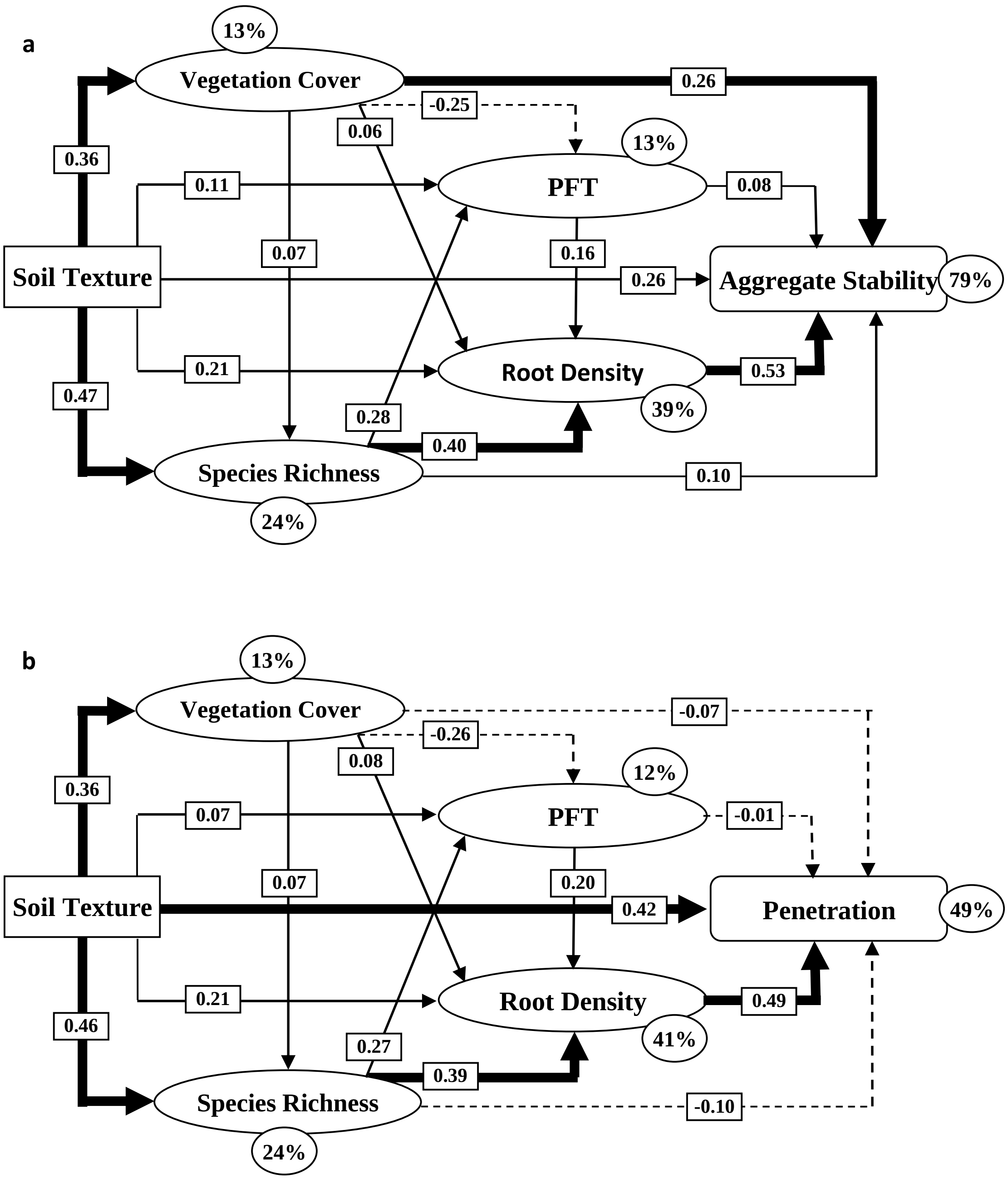

Fig. 3.S2. The path model outputs for the effects of soil texture "silt % and clay%", vegetation cover, species richness, root density and PFTs "root/shoot ratio, root length and root horizontal width" without accounting for intraspecific trait variability, on three soil stability measures. (a) soil aggregate stability (b) penetration resistance and (c) soil shear vane strength. Numbers on arrows are standardized path coefficients. Solid arrows indicate positive and dashed ones negative coefficients, bold arrows indicate significant standardized paths (P < 0.05); thin arrows indicate non-significant path coefficients (P > 0.05). Percentages close to the boxes indicate the variance explained by the model (R^2). The goodness-of-fit indices for the models are 0.45 for (a), 0.41 for (b) and 0.38 for (c).

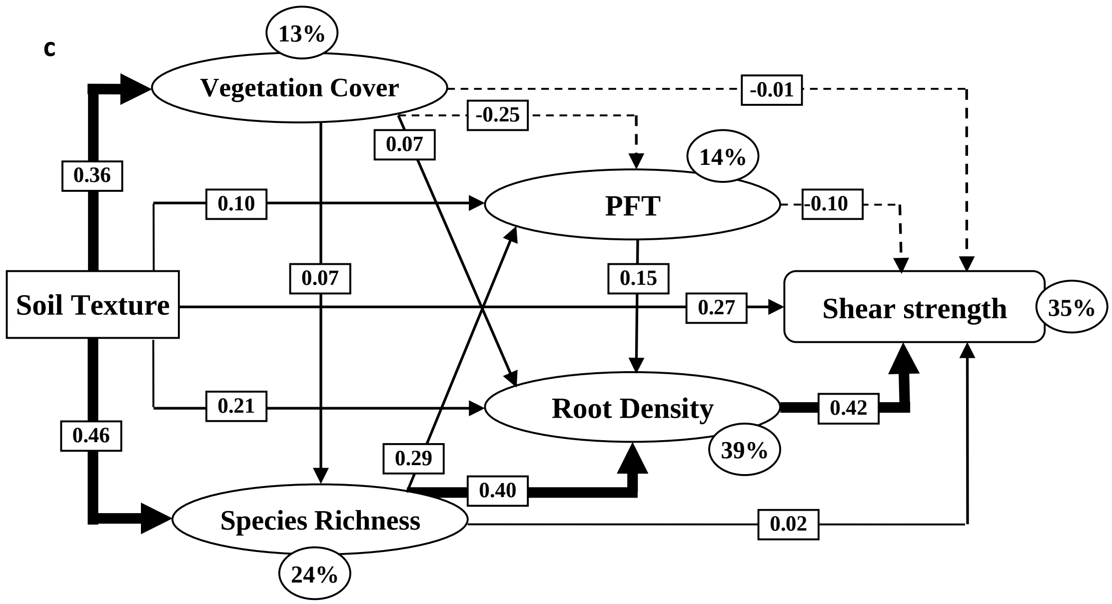

Fig. 3.S2 (cont.). The path model outputs for the effects of soil texture "silt % and clay%", vegetation cover, species richness, root density and PFTs "root/shoot ratio, root length and root horizontal width" without accounting for intraspecific trait variability, on three soil stability measures. (a) soil aggregate stability (b) penetration resistance and (c) soil shear vane strength. Numbers on arrows are standardized path coefficients. Solid arrows indicate positive and dashed ones negative coefficents, bold arrows indicate significant standardized paths ($P < 0.05$); thin arrows indicate non-significant path coefficients ($P > 0.05$). Percentages close to the boxes indicate the variance explained by the model (R^2). The goodness-of-fit indices for the models are 0.45 for (a), 0.41 for (b) and 0.38 for (c).

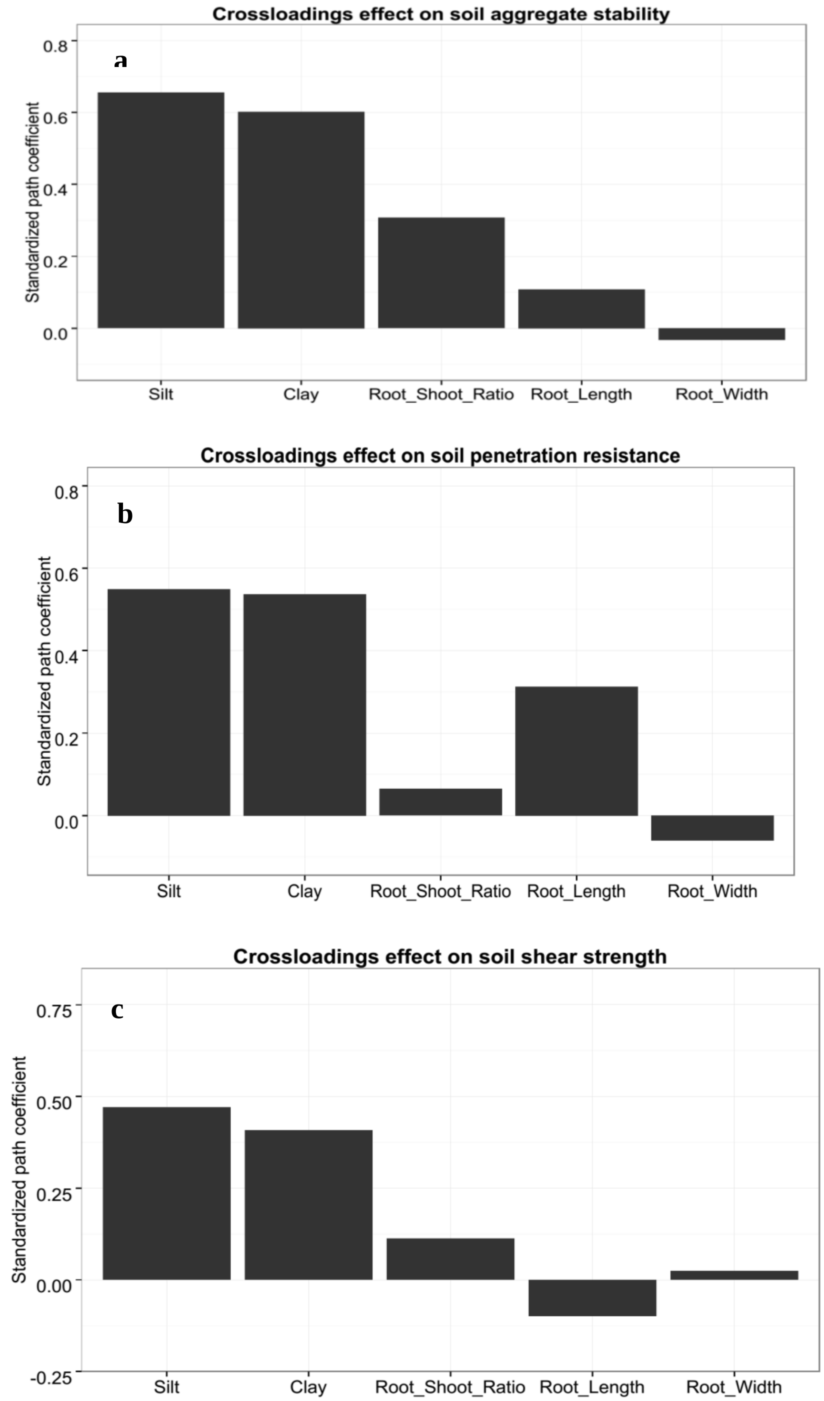

Fig. 3.S3. The path model crossloading effect of soil texture “silt % and clay %” and PFTs “root/shoot ratio, root length and root horizontal width” without accounting for intraspecific trait variability on (a) soil aggregate stability, (b) soil penetration resistance and (c) soil shear strength.

Table 3.S1. Results of the three path models of the effects of soil texture "silt % and clay%", vegetation cover, species richness, root density and PFTs "root/shoot ratio, root length and root horizontal width" **without** accounting for intraspecific trait variability, on three soil stability measures, (A) soil aggregate stability, (B) soil penetration resistance and (C) soil shear vane strength. Provided are the direct, indirect and total effects, unstandardized path coefficient (estimates), standard error of regression weight (S.E.) and level of significance for regression weight (P). Significant paths (P < 0.05) are given in bold.

			Effects			S.E.	*t* value	*P*
			Direct	Indirect	Total			
(A) Soil aggregate stability (goodness-of-fit = 0.45)								
Soil texture	→	**Vegetation cover**	**0.364**	**0.000**	**0.364**	**0.176**	**2.070**	**0.048**
Soil texture	→	**Species richness**	**0.460**	**0.025**	**0.485**	**0.180**	**2.550**	**0.017**
Soil texture	→	PFTs	0.114	0.043	0.157	0.219	0.522	0.606
Soil texture	→	Root density	0.2147	0.2478	0.4625	0.187	1.15	0.262
Soil texture	→	Aggregate stability	0.217	0.445	0.662	0.114	1.900	0.070
Vegetation cover	→	Species richness	0.068	0.000	0.068	0.185	2.010	0.136
Vegetation cover	→	PFTs	-0.251	0.018	-0.232	1.87	1.15	0.262
Vegetation cover	→	Root density	0.069	-0.011	0.058	0.173	0.403	0.690
Vegetation cover	→	**Aggregate stability**	**0.263**	**0.019**	**0.282**	**0.102**	**2.58**	**0.016**
Species richness	→	PFTs	0.279	0.000	0.279	0.210	1.33	0.195
Species richness	→	Root density	**0.405**	**0.045**	**0.451**	**0.184**	**2.200**	**0.037**
Species richness	→	Aggregate stability	0.0966	0.2604	0.357	0.1186	0.841	0.423
PFTs	→	Root density	0.1638	0.000	0.1638	0.167	0.982	0.335
PFTs	→	Aggregate stability	0.079	0.0865	0.1656	0.100	0.789	0.437
Root density	→	**Aggregate stability**	**0.5284**	**0.000**	**0.5284**	**0.117**	**4.48**	**<0.000**
(B) Soil penetration resistance (goodness-of-fit = 0.41)								
Soil texture	→	**Vegetation cover**	**0.364**	**0.000**	**0.364**	**0.176**	**2.070**	**0.048**
Soil texture	→	**Species richness**	**0.460**	**0.025**	**0.485**	**0.180**	**2.550**	**0.017**
Soil texture	→	PFTs	0.069	0.035	0.104	0.220	0.314	0.756
Soil texture	→	Root density	0.219	0.243	0.462	0.185	1.190	0.2457
Soil texture	→	**Penetration**	**0.417**	**0.153**	**0.571**	**0.179**	**2.330**	**0.028**
Vegetation cover	→	Species richness	0.067	0.000	0.068	0.180	0.372	0.713
Vegetation cover	→	PFTs	-0.268	0.018	-0.250	0.198	-1.360	0.186
Vegetation cover	→	Root density	0.082	-0.024	0.0587	0.172	0.482	0.6338
Vegetation cover	→	Penetration	-0.073	0.023	-0.050	0.163	-0.450	0.656
Species richness	→	PFTs	0.276	0.0000	0.276	0.210	1.310	0.200
Species richness	→	**Root density**	**0.395**	**0.055**	**0.451**	**0.182**	**2.170**	**0.0399**
Species richness	→	Penetration	-0.094	0.220	0.126	0.188	-0.503	0.6194
PFTs	→	Root density	0.202	0.000	0.202	0.164	1.230	0.2303
PFTs	→	Penetration	-0.002	0.099	0.097	0.160	-0.013	0.9895
Root density	→	**Penetration**	**0.490**	**0.000**	**0.490**	**0.189**	**2.590**	**0.016**
(C) Soil shear vane strength (goodness-of-fit = 0.38)								
Soil texture	→	**Vegetation cover**	**0.365**	**0.000**	**0.365**	**0.176**	**2.070**	**0.048**
Soil texture	→	**Species richness**	**0.460**	**0.025**	**0.485**	**0.180**	**2.550**	**0.017**
Soil texture	→	PFTs	0.103	0.052	0.1556	0.218	0.476	0.638
Soil texture	→	Root density	0.216	0.245	0.462	0.187	1.160	0.258
Soil texture	→	Shear strength	0.274	0.190	0.464	0.202	1.360	0.188
Vegetation cover	→	Species richness	0.066	0.000	0.066	0.180	0.370	0.714
Vegetation cover	→	PFTs	-0.252	0.019	-0.233	0.196	-1.290	0.209
Vegetation cover	→	Root density	0.068	-0.010	0.058	0.173	0.396	0.695
Vegetation cover	→	Shear strength	-0.007	0.049	0.042	0.183	-0.039	0.969
Species richness	→	PFTs	0.298	0.000	0.298	0.209	1.430	0.165
Species richness	→	**Root density**	**0.403**	**0.047**	**0.451**	**0.185**	**2.180**	**0.039**
Species richness	→	Shear strength	0.020	0.163	0.184	0.213	0.096	0.924
PFTs	→	Root density	0.158	0.000	0.159	0.168	0.947	0.352
PFTs	→	Shear strength	-0.100	0.068	-0.032	0.180	-0.557	0.582
Root density	→	**Shear strength**	**0.429**	**0.000**	**0.429**	**0.313**	**2.118**	**0.046**

Table 3.S2. Results of the three path models of the effects of soil texture "silt % and clay%", vegetation cover, species richness, root density and PFTs "root/shoot ratio, root length and root horizontal width" **with** accounting for intraspecific trait variability, on three soil stability measures, (A) soil aggregate stability, (B) soil penetration resistance and (C) soil shear vane strength. Provided are the direct, indirect and total effects, unstandardized path coefficient (estimates), standard error of regression weight (S.E.) and level of significance for regression weight (P). Significant paths (P < 0.05) are given in bold.

			Effects			S.E.	*t* value	*P*
			Direct	Indirect	Total			
(A) Soil aggregate stability (goodness-of-fit = 0.58)								
Soil texture	→	**Vegetation cover**	**0.364**	**0.000**	**0.364**	**0.176**	**2.070**	**0.048**
Soil texture	→	**Species richness**	**0.460**	**0.025**	**0.485**	**0.180**	**2.550**	**0.017**
Soil texture	→	PFTs	**0.385**	**0.127**	**0.512**	**0.193**	**2.120**	**0.041**
Soil texture	→	Root density	-0.043	0.506	0.463	0.136	-0.318	0.753
Soil texture	→	Aggregate stability	0.217	0.445	**0.662**	0.114	1.900	0.070
Vegetation cover	→	Species richness	0.068	0.000	0.068	0.185	2.010	0.136
Vegetation cover	→	PFTs	-0.030	0.019	-0.011	0.174	-0.174	0.863
Vegetation cover	→	Root density	0.051	0.009	0.059	0.114	0.444	0.661
Vegetation cover	→	**Aggregate stability**	**0.257**	**0.027**	**0.284**	**0.096**	**2.670**	**0.013**
Species richness	→	PFTs	**0.284**	**0.000**	**0.284**	**0.185**	**2.010**	**0.042**
Species richness	→	Root density	0.246	0.204	**0.451**	0.126	1.950	0.063
Species richness	→	Aggregate stability	0.127	0.231	0.357	0.114	1.110	0.279
PFTs	→	Root density	**0.719**	**0.000**	**0.719**	**0.128**	**5.610**	**<0.000**
PFTs	→	Aggregate stability	0.242	0.258	**0.500**	0.162	1.490	0.149
Root density	→	**Aggregate stability**	**0.559**	**0.000**	**0.559**	**0.168**	**2.130**	**0.044**
(B) Soil penetration resistance (goodness-of-fit = 0.54)								
Soil texture	→	**Vegetation cover**	**0.364**	**0.000**	**0.364**	**0.176**	**2.070**	**0.048**
Soil texture	→	**Species richness**	**0.460**	**0.025**	**0.485**	**0.180**	**2.550**	**0.017**
Soil texture	→	PFTs	**0.395**	**0.125**	**0.520**	**0.191**	**2.060**	**0.049**
Soil texture	→	Root density	-0.053	0.516	**0.463**	0.135	-0.394	0.697
Soil texture	→	**Penetration**	**0.443**	**0.128**	**0.571**	**0.188**	**2.360**	**0.027**
Vegetation cover	→	Species richness	0.068	0.000	0.068	0.180	0.378	0.709
Vegetation cover	→	PFTs	-0.041	0.020	-0.022	0.172	-0.240	0.812
Vegetation cover	→	Root density	0.059	0.001	0.060	0.113	0.521	0.607
Vegetation cover	→	Penetration	-0.080	0.031	-0.049	0.157	-0.506	0.617
Species richness	→	PFTs	**0.289**	**0.000**	**0.289**	**0.183**	**2.114**	**0.047**
Species richness	→	**Root density**	0.240	0.210	**0.451**	0.126	1.910	0.068
Species richness	→	Penetration	-0.102	0.228	0.126	0.186	-0.546	0.590
PFTs	→	Root density	**0.728**	**0.000**	**0.728**	**0.129**	**5.660**	**<0.000**
PFTs	→	Penetration	-0.123	0.426	0.302	0.268	-0.460	0.650
Root density	→	**Penetration**	**0.585**	**0.000**	**0.585**	**0.276**	**2.120**	**0.045**
(C) Soil shear vane strength (goodness-of-fit = 0.52)								
Soil texture	→	**Vegetation cover**	**0.365**	**0.000**	**0.365**	**0.176**	**2.070**	**0.048**
Soil texture	→	**Species richness**	**0.460**	**0.025**	**0.485**	**0.180**	**2.550**	**0.017**
Soil texture	→	PFTs	**0.400**	**0.125**	**0.525**	**0.191**	**2.100**	**0.046**
Soil texture	→	Root density	-0.059	0.521	**0.463**	0.136	-0.433	0.669
Soil texture	→	Shear strength	0.305	0.158	**0.463**	0.213	1.430	0.164
Vegetation cover	→	Species richness	0.068	0.000	0.068	0.180	0.376	0.710
Vegetation cover	→	PFTs	-0.041	0.020	-0.022	0.172	-0.241	0.811
Vegetation cover	→	Root density	0.059	0.000	0.059	0.113	0.522	0.606
Vegetation cover	→	Shear strength	0.009	0.035	0.044	0.178	0.049	0.961
Species richness	→	PFTs	**0.290**	**0.000**	**0.290**	**0.183**	**2.119**	**0.045**
Species richness	→	**Root density**	0.239	0.212	**0.451**	0.126	1.900	0.069
Species richness	→	Shear strength	-0.009	0.194	0.185	0.210	-0.042	0.967
PFTs	→	Root density	**0.732**	**0.000**	**0.732**	**0.129**	**5.670**	**<0.000**
PFTs	→	Shear strength	-0.174	0.396	0.222	0.305	-0.570	0.574
Root density	→	**Shear strength**	**0.541**	**0.000**	**0.541**	**0.313**	**2.118**	**0.046**

Chapter 4: Extensive management of field margins enhances their potential to mitigate soil erosion

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Submitted to *Agriculture, Ecosystems and Environment*

Abstract

Soil erosion is a widespread problem in agricultural landscapes, particularly in regions with strong rainfall events. Vegetated field margins can mitigate negative impacts of soil erosion by trapping eroded material. Here we analyze how local management affects the trapping capacity of field margins in a monsoon region of South Korea, contrasting intensively and extensively managed field margins on both steep and shallow slopes. Prior to the beginning of monsoon season, we equipped a total of 12 sites representing three replicates for each of four different types of field margins ("intensive managed flat", "intensive managed steep", "extensive managed flat" and "extensive managed steep") with Astroturf mats. The mats (n = 15 / site) were placed before, within and after the field margin. Sediment was collected after each rain event until the end of the monsoon season.

The effect of management and slope on sediment trapping was analyzed using linear mixed effects models, using as response variable either the sediment collected within the field margin or the difference in sediment collected after and before the field margin. In all cases, there was a positive relation between rainfall and sediment collected. While there was no difference in the amount of sediment reaching the different field margin types, extensively managed field margins showed a large reduction in collected sediment before and after the field margins. This effect was particularly pronounced in steep field margins. We conclude that a field margin management promoting a dense vegetation cover is a key to mitigating negative effects of soil erosion in monsoon regions, particularly in field margins with steep slopes.

Keywords: Soil erosion, field margins, sediment retention, management, slope, agricultural landscape, monsoon.

4.1 Introduction

Soil erosion is a widespread problem in agricultural landscapes, especially in areas subjected to intensive rainfall events. Soil erosion has been intensifying in recent years (Pimentel *et al.*, 1995), and causes potentially sever reductions in productivity (Eswaran *et al.*, 2001). Due to the summer monsoon, East Asian countries such as South Korea receive a huge amount of rainfall, which impacts both the agriculture and economy (Chen *et al.*, 1988). These rains along with the human activities cause water erosion that in addition to production losses produces severe problems in agricultural landscapes, e.g. sedimentation downstream of fields in flood plains and water bodies, which as a result affects water quality (Van Oost *et al.*, 2007; Xu *et al.*, 2013). Water erosion is responsible for degradation of a total 441 M ha or 59% of the total degraded soil in Asia (Oldeman, 1994).

Preventing and controlling soil erosion can principally be achieved by reducing the erosive impact of rainfall and by maintaining soil infiltration rates, which consequently will prevent surface flow. This can be done using several methods; e.g. within the field via crop rotation and tillage practices (Raclot & Albergel, 2006; Wang *et al.*, 2010); by improving soil stability which will help in soil erosion control in the longer term (Barthès & Roose, 2002), or between fields by using vegetated field margins (Zheng, 2006; Wei *et al.*, 2014)..

Several studies have shown that field margins can assist in sediment retention by trapping as much as 70-90% of the inflowing sediment, consequently reducing sediment loads to rivers and streams (Duzant *et al.*, 2010). The vegetation of the field margin efficiently removes large heavy particles (Hickey & Doran, 2004). Owens *et al.* (2007), in their study on field margins in southwest England, found that field margins were effective in trapping the coarse sediment fractions, and that soil type, slope, land-use and management influence the amount of sediment that can be trapped by field margins. Heede (1990), in a study on natural vegetated buffer strips in pine forests in Arizona, showed that the vegetated buffer strips trapped 61 times more sediment than sites where buffer strips were missing.

Two important determinants of how effectively field margins mitigate the negative effects of soil erosion are the characteristics of their vegetation and the slope of the field margin. Vegetation traps sediments and protects soil against erosion mainly by reducing runoff and by increasing the infiltration rate into soil (Zheng, 2006; Fu *et al.*, 2011). Moreover, plants protect soil using their roots, which bind the soil particles via the root excretions (Traore *et al.*, 2000; Gyssels *et al.*, 2005; de Baets *et al.*, 2007), by reducing the raindrops' effect on the soil with their canopy (Gray & Sortir, 1996; Durán Zuazo *et al.*, 2008), acting as a physical barrier to change sediment flow at the soil surface (Van Dijk *et al.*, 1996; Lee *et al.*, 2000; Martínez *et al.*, 2006). The spatial distribution of vegetation along the slope is an important factor for reducing the sediment runoff (Lavee *et al.*, 1998; Calvo-Cases *et al.*, 2003; Francia Martínez *et al.*, 2006). While Abrahams *et al.* (1996) have shown that the effect of slope steepness on soil loss is complex, erosion is expected to increase as the slope steepens (Zheng, 2006; Fu *et al.*, 2011), as a result of the respective increase in velocity and volume of surface runoff (Ziadat &

Taimeh, 2013). The effect of slope is modulated by other factors like soil properties (Singer & Blackard, 1982), surface conditions (Martínez *et al.*, 2006) and vegetation cover (Singer & Blackard, 1982; Hancock *et al.*, 2015). While thus important elements exist for understanding how field margin vegetation structure and slope interact in mitigating erosion effects, there is a knowledge gap on how alternative management of the field margin translates into reduced or enhanced soil erosion effects.

The aim of this paper is therefore to investigate how the local management of field margins affects their potential to mitigate the negative effects of soil erosion in a monsoon area. In particular, we compare the amount of sediment trapped between intensively managed field margins (i.e. by cutting) and extensively managed field margins (no management for at least one year). First, we analyze the effects of the two field margin management intensities, on both shallow and steep slopes, on the sediment differences collected after and before the field margins, which is related to the net uptake or release of sediment of the field margin. Second, we analyze the amount of sediment collected within the different field margins, which will give us a wider picture on the amount of sediment that will be trapped by the different types of the field margins.

4.2 Materials and methods

4.2.1 Study site

The study was conducted in the Haean-myun catchment in the Kangwon Province located in the northeast of South Korea (128°05’ to 128°11’ E, 38°13’ to 38°20’ N; Fig. 4.1). Elevation in the study site varies from 500 to 750 m a.s.l. The mean annual air temperature is 10.5 ºC; the mean monthly temperature varies between -10 ºC in January and 27 ºC in August (1999 - 2013). The average precipitation is 1,500 mm, with 70% of the rain falling during the summer monsoon from July to August; with rainfall events > 50 mm/day being common (Fig. 4.2) (Berger *et al.*, 2013). The catchment is part of the watershed of the Soyang Lake, which is the largest reservoir in South Korea (Kim, B *et al.*, 2000). The Haean-myun catchment is a major agricultural hotspot that substantially affects the trophic state of the reservoir (Park *et al.*, 2010). The total catchment area is 64 km² with 58% of the catchment classified as forested mountains and 30% as agricultural areas (22% dryland fields and 8% rice paddy fields), while the remaining 12% are residential areas and semi-natural areas including grassland, field margins, riparian areas, channels, and farm roads (Seo *et al.*, 2014). The topography of the research area is characterized by flat areas and moderately steep slopes in the center of the catchment and steep slopes at the forest edges. The terrain is highly complex with a variety of different hill slopes and flow directions.

In the Haean-myun catchment, soils are strongly affected by human activities; especially dry fields are modified by the addition of the excavated materials from nearby mountain slopes in order to offset annual erosion losses (Park *et al.*, 2010). Average annual soil erosion rate ranges from 30 to 54 (t $ha^{-1}yr^{-1}$) (Arnhold *et al.*, 2014).

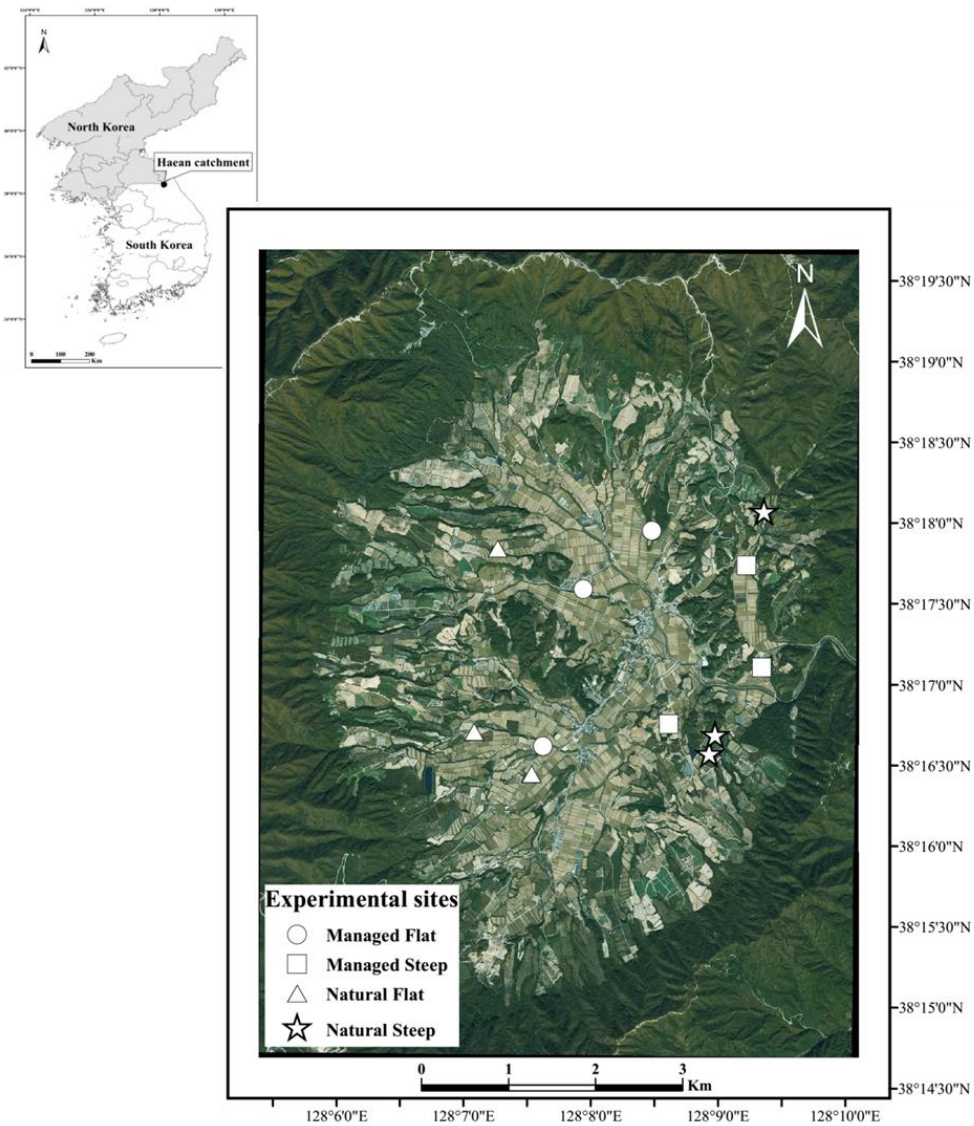

Fig. 4.1. The 12 sampling sites for the sediment trapping in Haean-myun catchment.

4.2.2 Study design and sediment collection

To test the effect of management ("intensively managed", hereafter "managed" or "extensively managed", hereafter "natural") and slope degree ("steep" or "flat") of the field margin in erosion control, 12 sites were installed in Haean-myun catchment for our four different combinations, which are "managed-flat", "managed-steep", "natural-flat" and "natural-steep" with three replicates for each treatment (Fig. 4.1). Managed field margins were continuously managed by cutting for the whole season, while the natural ones were left without any type of management. Steep slopes were selected to have approximately a 35° slope, while the flat slopes ranged from 1° to 2°. To reduce potential confounding factors other than management and slope, all sites were selected to be next to radish fields, which are considered to have the highest average annual soil erosion rate within our study catchment (Arnhold *et al.*, 2014), with the same age and field slope degree from 2° to 5°.

To trap the sediment that reached the field margins, Astroturf mats with a size of 34 cm x 25 cm (850 cm^2) (for more details see (Lambert & Walling, 1987; Walling & Owens, 2003), were installed at three levels: upslope, immediately before the field margin to quantify the sediments that reach it, in the middle of the field margin to quantify the locally trapped sediments, and after the field margin at the downslope edge to quantify the sediments that leave the field margin to the next field or to the stream. In total, 15 mats were installed at each site, with five mats at each level (Fig. 4.3). Mats were installed in May 2013 and were monitored after each rain event until the end of the monsoon season. Mats containing sediments were collected and transferred to the laboratory, where the sediments were dried at room temperature, removed from the mats and weighed.

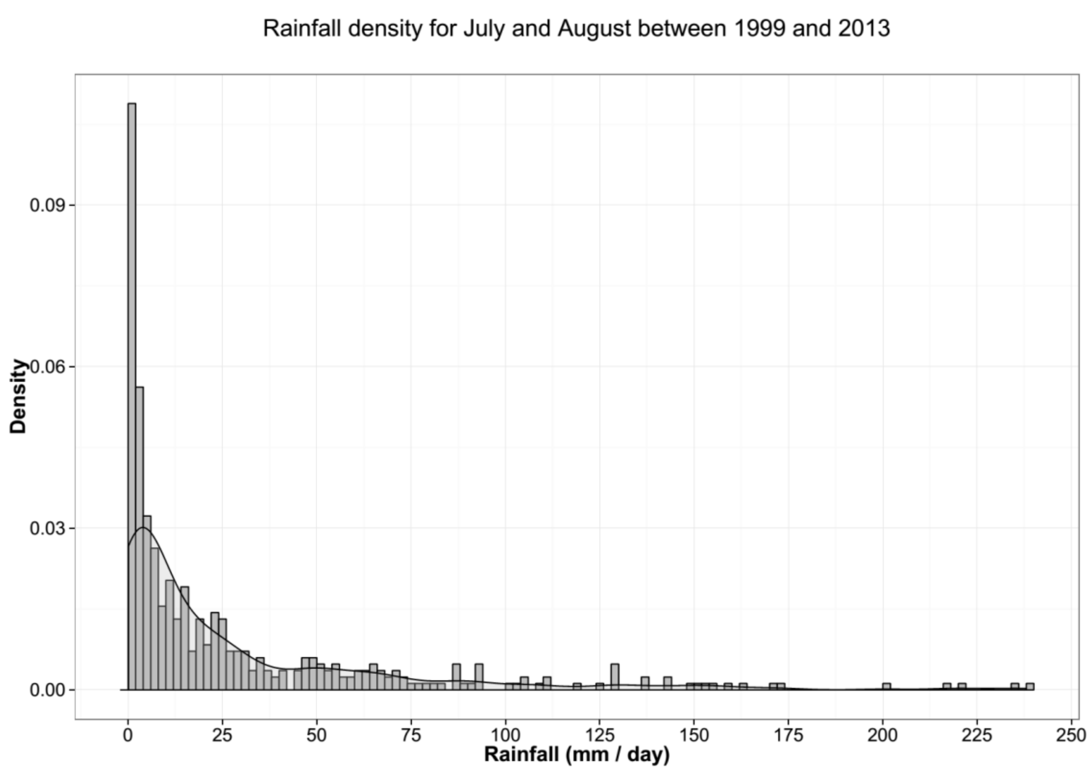

Fig. 4.2. Rainfall frequency distribution in Haean-myun catchment for July and August between 1999 and 2013.

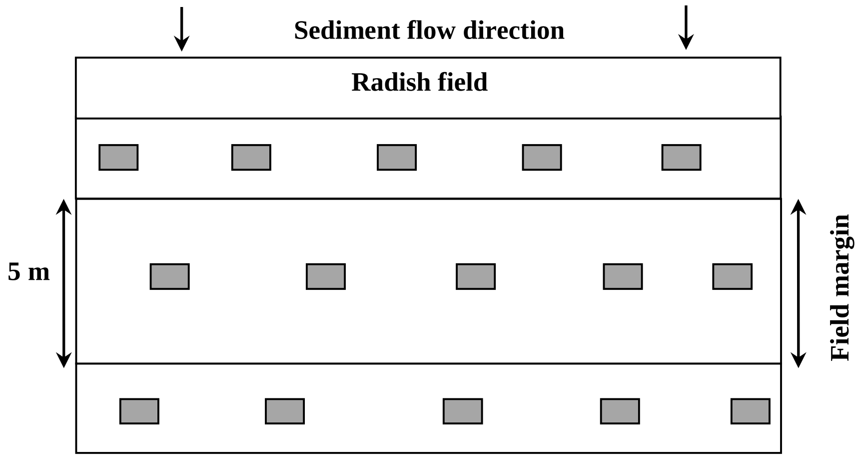

Fig. 4.3. Schematic diagram showing the location of the Astroturf mats (grey squares) before, within and after the field margin. All selected field margins had a width of 5 m and were located next to radish fields.

4.2.3 Statistical analysis

We used linear mixed effects models (LME) to analyze three response variables: (1) the sediment amount collected before the field margin, with "rainfall amount" and "field margin type" as well as their interaction as fixed effects, to test whether the different field margin types received different amounts of sediment; (2) the difference of sediment collected after and before the field margin, with "rainfall amount", "slope", "management" and the two-way and three-way interactions between these as fixed effects, to quantify the main and interaction effects of management and slope on sediment retention of field margins ; (3) the sediment amount collected within the field margin with "rainfall amount" and "field margin type" as well as their interaction as fixed effects to yield additional insights on the sediment retention and release within field margins. In all cases, the field margin ID was used as a random variable. Backward variable selection from the full model with AIC was done on models fitted with maximum likelihood; final parameter estimates were done with restricted maximum likelihood (REML).

The variance of model residuals increased with the amount of rainfall. We accounted for this heteroscedasticity by modelling residual variance as an exponential function of rainfall.

All the statistical analyses were performed with R, version 3.1.2 (R Development Core Team, 2014), using package "*nlme*" (Pinheiro *et al.*, 2013).

4.3 Results

From May to August 2013, Haean-myun catchment received a total amount of 740 mm rainfall in 18 different rain events, where rainfall ranged between 8 mm to 107 mm/event (Table 4.S1). In all cases, we found a clear positive relation between rainfall, and the sediment amount captured by the Astroturf mats (Figs. 4.4a, 4.5a, 4.6a and Fig. 4.S1).

There was no statistically significant difference in the amount of sediment that reached the four field margin types (Table 4.1). Averaged over all rainfall events, the mean sediment that reached the four field margin types was 1.2 ± 0.13 g/cm^2 for the managed flat, 1.18 ± 0.13 g/cm^2 for the managed steep, 1.18 ± 0.13 g/cm^2 for the natural flat, and 1.22 ± 0.14 g/cm^2 for the natural steep margins (Figs. 4.4a and 4.4b); indicating that we were successful in keeping upslope factors potentially affecting sediment movement constant.

4.3.1 Difference in sediment collected after and before the field margins

Except for managed flat field margins, the differences between sediment collected after and before the field margin increased with increasing rainfall (Fig. 4.5a). However, while managed steep margins acted as a source of sediments, natural field margins acted as a sink (Fig. 4.5b): averaged over all rainfall events, the mean sediment difference in the managed flat margins was 0.001 ± 0.003 g/cm^2, in the managed steep margins 0.032 ± 0.004 g/cm^2, in the natural flat -0.070 ± 0.005 g/cm^2, and in the natural steep -0.064 ± 0.005 g/cm^2 (Fig. 4.5b).

The best linear mixed effect model explained 91% of the variance of the sediment difference collected after and before the field margin (Table 4.2), and contained a significant three-way interaction between rainfall amount, management and slope (P = 0.048, Fig. 4.S2).

4.3.2 Sediment collected within the field margins

Within field margins, Astroturf mats in the natural field margins trapped more sediment than those in the managed field margins. Differences between natural and managed margins were pronounced in steep slopes (Figure, 4.6a). Averaged over rainfall events, the mean sediment collected within the managed flat margins was 1.19 ± 0.14 g/cm^2, in the managed steep margins 0.74 ± 0.08g/cm^2, in the natural flat margins 1.30 ± 0.15 g/cm^2 and in the natural steep margins 1.43 ± 0.16g/cm^2 (Fig. 4.6b).

The best linear mixed effect model explained 71% of the variance of the sediment collected within the field margins (Table 4.3) and contained statistically significant interactions between the effect of rainfall and the different field margin types. The increase of sediment collection with rainfall was lowest in the managed steep slopes. All other field margin types had higher increases of sediment collection with rainfall, in the case of steep natural margins; the increase of trapped sediment with rainfall was almost twice as high as in managed steep margins (Fig. 4.6a, Table 4.3 and Fig. 4.S3).

Overall, we found that natural field margins trapped substantial amounts of sediment, leading to a net reduction of sediment load in runoff from the field margin relative to the water reaching the field margin. The benefits of natural field margins increased with rainfall intensity and slope.

Table 4.1. Linear mixed effect model for the effect of rainfall on the sediment collected before field margins.

	Estimate	**SE**	**DF**	***t* value**	***P***	**AIC**	***R*^{2}**
(Intercept)	0.222	0.065	143	3.43	0.001**	219	0.65
Rainfall	**0.023**	**0.001**	**143**	**19.99**	**<0.001*** **		

Significance codes: *** *P* < 0.001, ** *P* <0.01, * *P* <0.05. Statistically significant variables are indicated in bold

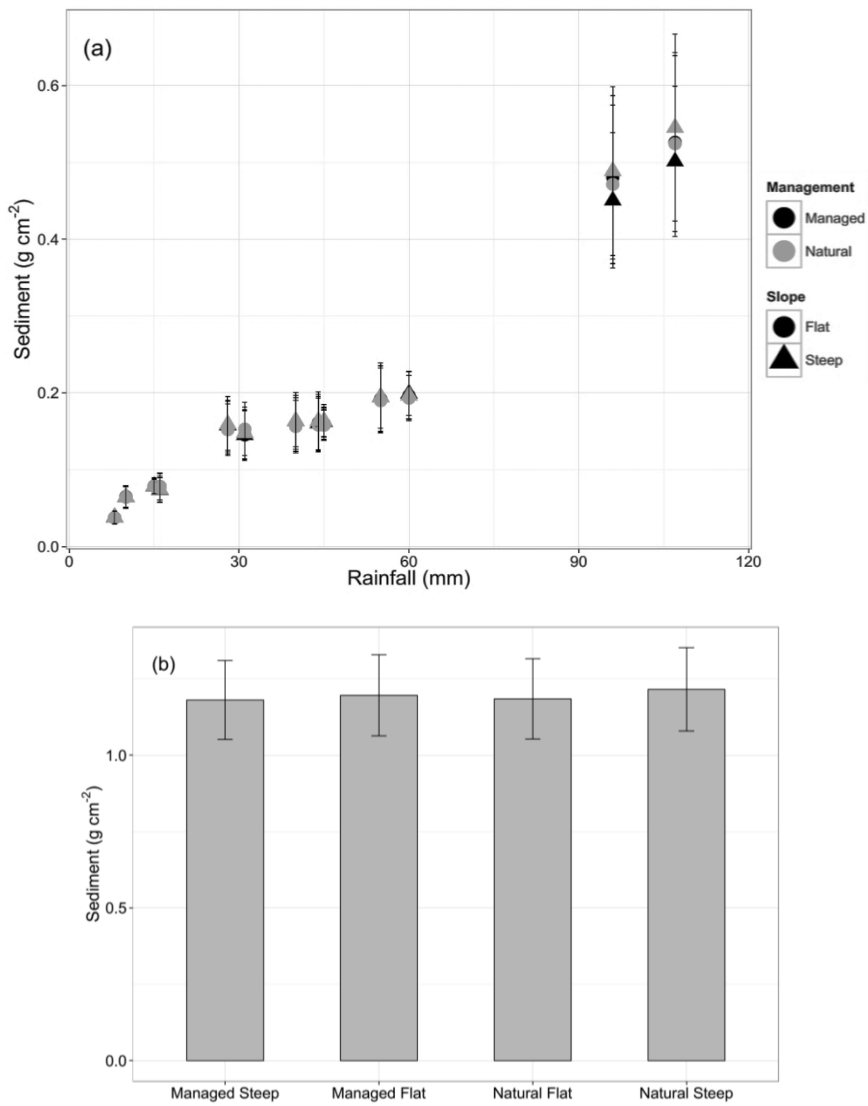

Fig. 4.4. Sediment collected before the field margin in the four different field margin types at different rain events, (a) relation between sediment collected before the field margin at different types and the rainfall and (b) average amount of the sediment collected before the field margin for the four different types.

Table 4.2. Linear mixed effect model for the effect of rainfall, slope and management on the difference in sediment collected after and before field margins.

	Estimate	**SE**	**DF**	***t* value**	***P***	**AIC**	**R^2**
(Intercept)	-0.032	0.038	140.000	-0.825	0.411		
Rainfall	0.001	0.001	140.000	1.027	0.306		
Steep	0.062	0.054	8.000	1.144	0.286		
Natural	-0.095	0.054	8.000	-1.761	0.116		
Rainfall *Steep	**0.004**	**0.001**	**140.000**	**2.663**	**0.009****	- 68.4	0.91
Rainfall*Natural	**-0.009**	**0.001**	**140.000**	**-7.112**	**<0.001*****		
Slope*Natural	-0.012	0.077	8.000	-0.161	0.876		
Rainfall*Steep*Natural	**-0.004**	**0.002**	**140.000**	**-1.987**	**0.048***		

Significance codes: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$. Statistically significant variables are indicated in bold

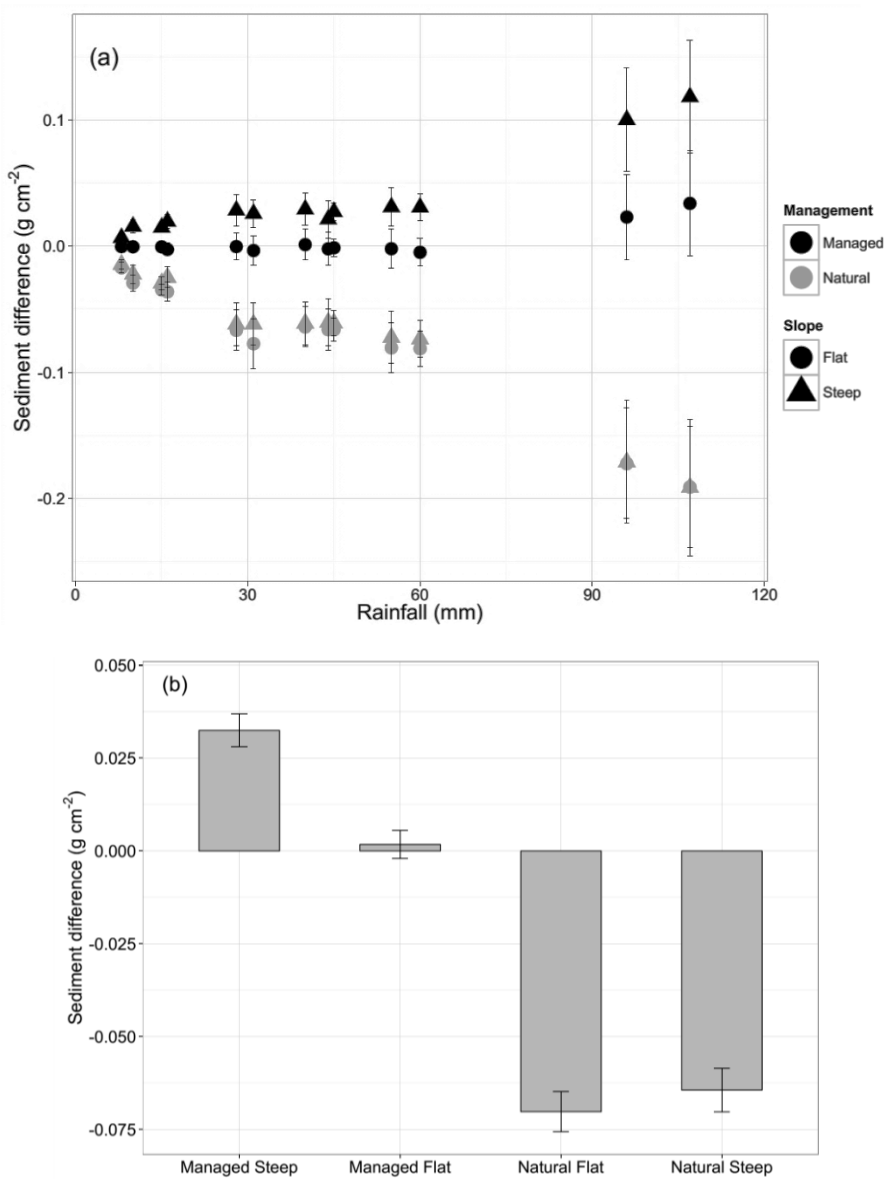

Fig. 4.5. Difference between sediment collected after and before the field margin in four different field margin types at different rain events.

Table 4.3. Linear mixed effect model for the effect of rainfall and field margin type on the sediment collected within field margins.

	Estimate	SE	DF	*t* value	*P*	AIC	R^2
(Intercept)	0.107	0.128	140.000	0.832	0.407	264	0.71
Rainfall	**0.015**	**0.002**	**140.000**	**6.316**	**<0.001*****		
Managed Flat	0.039	0.182	8.000	0.214	0.836		
Natural Steep	0.112	0.182	8.000	0.614	0.556		
Natural Flat	0.111	0.182	8.000	0.612	0.557		
Rainfall* Managed Flat	**0.010**	**0.003**	**140.000**	**2.946**	**0.004****		
Rainfall* Natural Steep	**0.014**	**0.003**	**140.000**	**4.131**	**<0.001*****		
Rainfall* Natural Flat	**0.011**	**0.003**	**140.000**	**3.209**	**0.002****		

Significance codes: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$. Statistically significant variables are indicated in bold

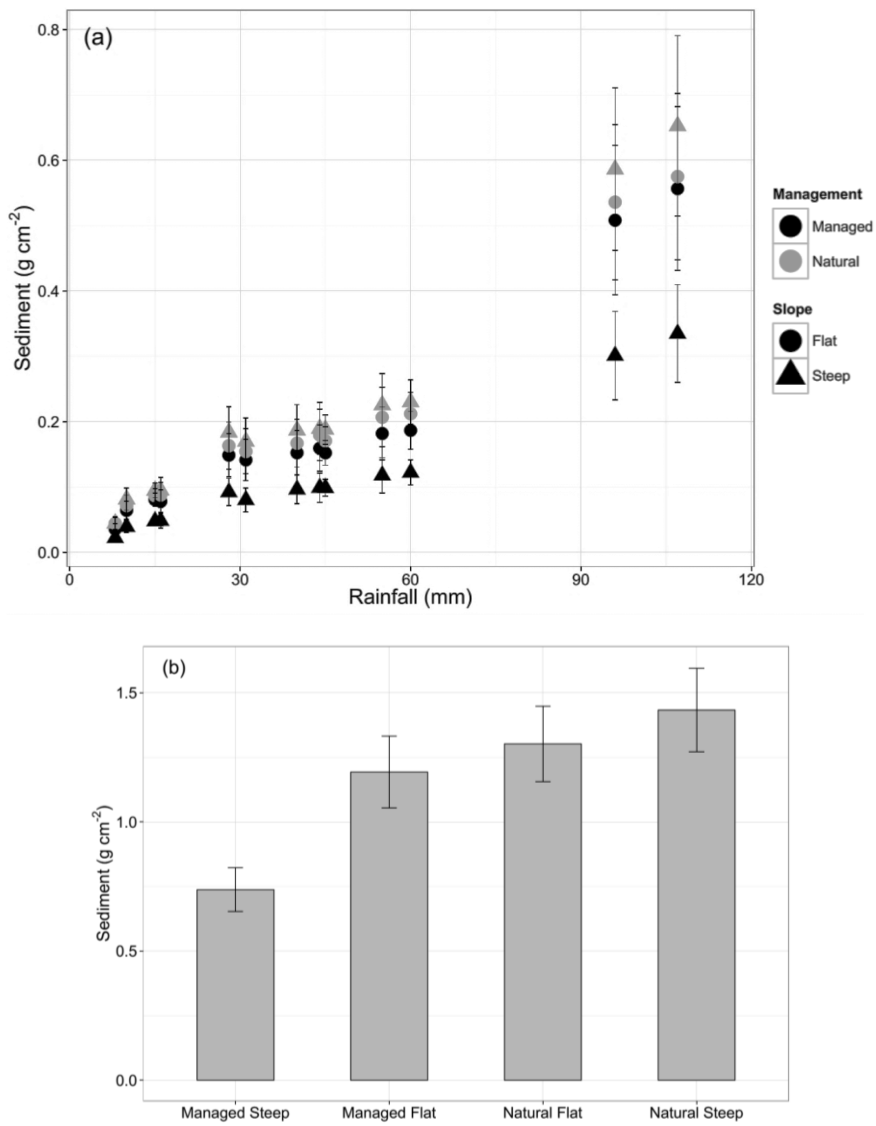

Fig. 4.6. Sediment collected within the field margin in the four different field margin types at different rain events, (a) relation between sediment collected within the field margin at different types and the rainfall and (b) average amount of the sediment collected before the field margin for the four different types.

4.4 Discussion

The current study is one of the few studies investigating the effect of field margin management on the potential of field margins to mitigate negative impacts of soil erosion, a key problem particularly in monsoon agricultural landscapes. We examined the combined effect of field margin management ("natural" or "managed") and field margin slope ("flat" or "steep") on sediment trapping in three different levels, i.e. before, within, and after the field margin, after each rain event during the monsoon season in an agricultural landscape of South Korea. Our results highlight that natural field margins can substantially reduce the amount of sediments in runoff, compared to the managed field margins, which on steep slopes may even increase sediment in downstream runoff.

4.4.1 Effect of rainfall amount on sediment collection

We found a positive relationship between rainfall amount and the sediments collected at the different levels of sediment collection before, within, and after the field margin, with a near linear increase of sediment deposition with rainfall amount for all field margin types (Figs. 4.4a, 4.6a and Fig. 4.S1). This result is well in line with several other studies. In a study that also used Astroturf mats for sediment collection, conducted in arable fields in England, equally showed a positive linear relation between rainfall and sediment deposition (Duzant *et al.*, 2010). Arnaez *et al.* (2007), in their study on agricultural vineyards in Spain, reported a linear relationship between rainfall intensity and soil erosion rates (R^2 = 0.76).Wei *et al.* (2014), reported that water erosion rates are affected markedly by the occurrence, characteristics, and distribution of rain events. Nearing *et al.* (2005), showed that the variability of rainfall serves key functions in the generation of water erosion. According to a study on the Loess Plateau in China, the rainfall amount is significantly affecting soil erosion intensity (Sun *et al.*, 2013).

4.4.2 Effect of vegetation cover on sediment collection

Our results showed that natural field margins, with comparatively high and dense vegetation cover, contributed to soil erosion control by trapping sediment. In agreement with our results, Sun *et al.* (2013) showed that soil erosion significantly declined by increasing vegetation cover. Similar results have been reported e.g. by Fu *et al.* (2011), who demonstrated that improving vegetation cover in areas that are susceptible to soil erosion improve soil erosion control.

4.4.3 Effect of slope degree on the sediment collection

For the effect of the slope on sediment trapping, our results showed the importance of the slope degree, but only in combination with management effect, i.e. in field margins with dense vegetation cover there was little difference in sediment trapping between shallow and steep slopes (Fig. 4.4a and Fig. 4.S2). Moreover, for flat slopes there was no big difference in the sediment collected within either the natural or managed field margins, but in steep slopes, natural field margins trapped more sediment than managed field margins (Fig. 4.6a). According to Fu *et al.* (2011), erosion increases as a function of slope, but this effect is also influenced by other factors like the vegetation cover (Hancock *et al.*, 2015), since dense vegetation may sufficiently reduce the increased runoff water velocity in steep slopes. In an experimental field study, Zheng (2006) showed that while over 90% of the erosion came from slopes without vegetation cover, low erosion occurred in slopes that were covered by dense vegetation.

4.4.4 Effectiveness of the Astroturf mats in sediment trapping

We used the Astroturf mats for sediment collection, because they can represent the natural ground surface well due to their rough surface and their pliability, and they allow for removing sediment easily (Steiger *et al.*, 2003). Furthermore, they provide an easy and fast way to illustrate the effect of soil erosion to local farmers and also allow them to monitor erosion themselves. Even though the Astroturf mats allowed to clearly identify effects of rainfall amount, management and slope on sediment trapping in our study, they have some limitations, for example they can have very low efficiency to trap small soil fractions (Deletic, 1999). Furthermore, sediment can bypass the mats if they are full of sediment, so mats need to be checked on a regular basis to replace mats that are full of sediment. Regardless of the limitations of using the Astroturf mats to trap sediment within the agricultural field margins, results obtained by this method can be calibrated to predict the sediment amount that can be trapped within the field margins on the catchment scale using the modified Morgan–Morgan–Finney erosion model (MMF) (Morgan & Duzant, 2008) that predicts the runoff and soil loss leaving each field below the field margin. Duzant *et al.* (2010), showed that erosion data that collected from field margins using the Astroturf mats can be used to simulate the effectiveness of field margins using the MMF model, when the field margin area that effectively contribute to soil erosion is defined from field observation.

4.4.5 Conclusions

The current study demonstrates the important role of field margin management and slope degree in mitigating soil erosion in a monsoon agricultural landscape. Particularly on steep slopes, a field margin management that promotes a dense vegetation cover is important for improving sediment retention in the field margins and thereby reducing negative effects downslope.

4.5 Acknowledgements

This work is part of the International Research Training Group “Complex TERRain and ECOlogical Heterogeneity” (TERRECO) (GRK 1565/1) funded by the German Research Foundation (DFG). We thank Sebastian Arnhold for supporting us in the field and the lab work, Bernd Huwe for his comments and suggestions on our field protocol and John Tenhunen for his comments and coordination of the TERRECO fieldwork.

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4.7 Supplementary materials

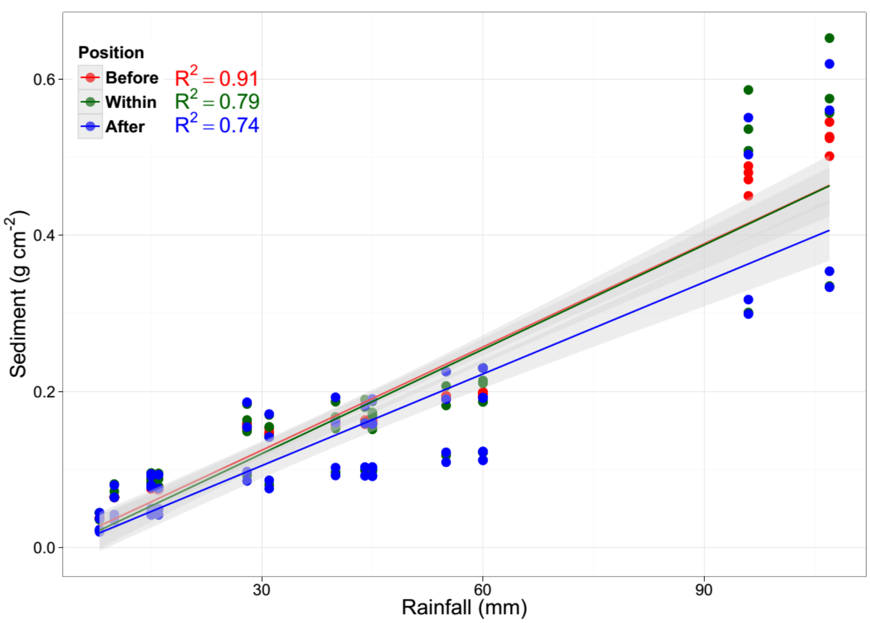

Fig. 4.S1. The relationship between sedimentation and rainfall in the 12 study sites at different positions. The R^2 and for these relationships are (0.91, 0.79 and 0.74) for sediment collected before, within and after the field margins, respectively ($P < 0.001$ in all cases).

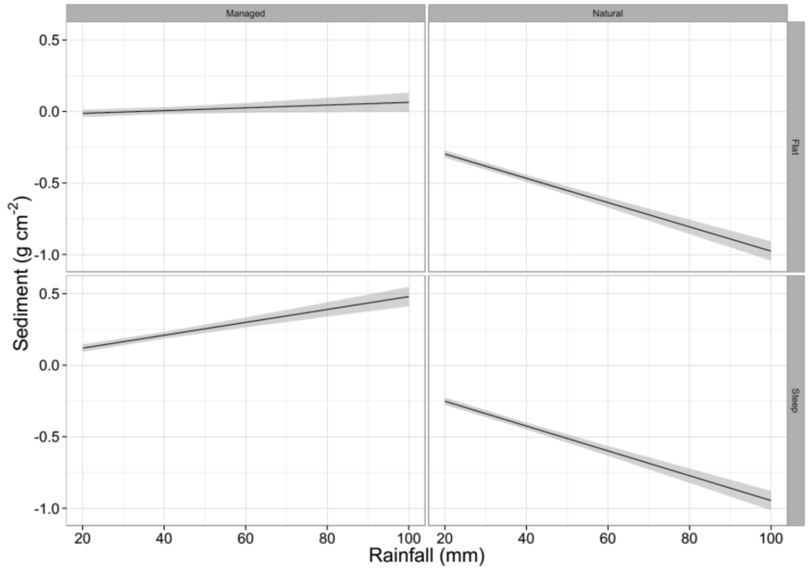

Fig. 4.S2. The effect of three-way interaction between rainfall amount, management and slope of field margin on the difference in sediment collected after and before field margins.

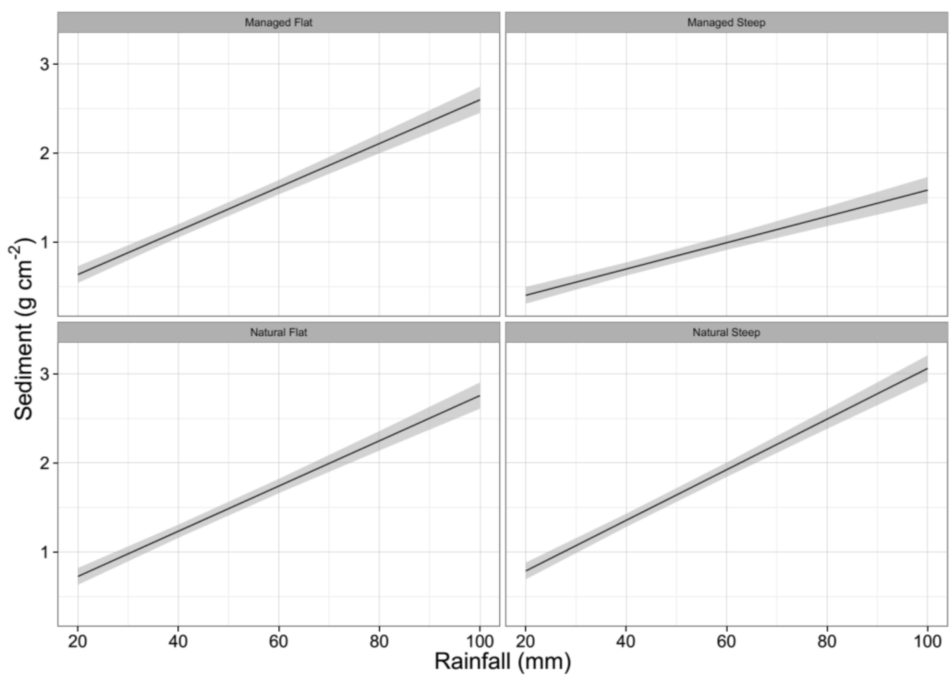

Fig. 4.S3. The effect of two-way interaction between rainfall amount and type field margin on the sediment collected within field margins.

Table 4.S1. Average amount of sediment deposited on the Astroturf mats for each rain event in the different field margins' type at different positions "before, within and after".

Rain event	Rainfall (mm)	Field margin type	Sediment deposition rate at different positions of the field margin (g cm^{-2})		
			Before	Within	After
1	10	Managed Steep	0.064 (0.05)	0.039 (0.04)	0.080 (0.06)
1	10	Managed Flat	0.065 (0.05)	0.064 (0.05)	0.064 (0.05)
1	10	Natural Flat	0.064 (0.05)	0.072 (0.06)	0.035 (0.03)
1	10	Natural Steep	0.065 (0.06)	0.081 (0.07)	0.042 (0.03)
2	15	Managed Steep	0.078 (0.06)	0.048 (0.04)	0.094 (0.07)
2	15	Managed Flat	0.079 (0.07)	0.078 (0.07)	0.077 (0.07)
2	15	Natural Flat	0.078 (0.07)	0.086 (0.07)	0.042 (0.04)
2	15	Natural Steep	0.076 (0.07)	0.095 (0.08)	0.049 (0.04)
3	8	Managed Steep	0.038 (0.03)	0.022 (0.02)	0.045 (0.03)
3	8	Managed Flat	0.037 (0.03)	0.036 (0.03)	0.037 (0.03)
3	8	Natural Flat	0.037 (0.03)	0.044 (0.04)	0.020 (0.02)
3	8	Natural Steep	0.038 (0.03)	0.045 (0.04)	0.023 (0.02)
4	28	Managed Steep	0.158 (0.13)	0.092 (0.08)	0.186 (0.14)
4	28	Managed Flat	0.155 (0.13)	0.149 (0.13)	0.155 (0.13)
4	28	Natural Flat	0.152 (0.13)	0.163 (0.14)	0.085 (0.07)
4	28	Natural Steep	0.159 (0.14)	0.184 (0.15)	0.097 (0.08)
5	40	Managed Steep	0.163 (0.13)	0.097 (0.09)	0.193 (0.15)
5	40	Managed Flat	0.159 (0.14)	0.153 (0.13)	0.160 (0.14)
5	40	Natural Flat	0.156 (0.13)	0.167 (0.14)	0.092 (0.08)
5	40	Natural Steep	0.164 (0.14)	0.187 (0.15)	0.103 (0.09)
6	15	Managed Steep	0.082 (0.06)	0.048 (0.04)	0.092 (0.07)
6	15	Managed Flat	0.079 (0.07)	0.084 (0.08)	0.080 (0.07)
6	15	Natural Flat	0.079 (0.07)	0.086 (0.07)	0.047 (0.04)
6	15	Natural Steep	0.085 (0.08)	0.095 (0.08)	0.050 (0.04)
7	107	Managed Steep	0.501 (0.38)	0.335 (0.29)	0.620 (0.50)
7	107	Managed Flat	0.527 (0.45)	0.557 (0.49)	0.560 (0.48)
7	107	Natural Flat	0.524 (0.44)	0.575 (0.49)	0.334 (0.28)
7	107	Natural Steep	0.545 (0.47)	0.653 (0.53)	0.354 (0.29)
8	31	Managed Steep	0.145 (0.12)	0.080 (0.07)	0.171 (0.14)
8	31	Managed Flat	0.145 (0.13)	0.142 (0.12)	0.142 (0.12)
8	31	Natural Flat	0.153 (0.13)	0.155 (0.13)	0.076 (0.06)
8	31	Natural Steep	0.148 (0.13)	0.170 (0.14)	0.086 (0.07)
9	45	Managed Steep	0.163 (0.13)	0.099 (0.09)	0.191 (0.15)
9	45	Managed Flat	0.159 (0.14)	0.154 (0.13)	0.159 (0.14)
9	45	Natural Flat	0.157 (0.13)	0.170 (0.14)	0.092 (0.08)
9	45	Natural Steep	0.164 (0.14)	0.187 (0.15)	0.103 (0.09)
10	45	Managed Steep	0.162 (0.13)	0.099 (0.09)	0.189 (0.15)
10	45	Managed Flat	0.161 (0.14)	0.152 (0.13)	0.158 (0.14)

Rain event	Rainfall (mm)	Field margin type	Sediment deposition rate at different positions of the field margin (g cm^{-2})		
			Before	Within	After
10	45	Natural Flat	0.159 (0.14)	0.170 (0.14)	0.092 (0.08)
10	45	Natural Steep	0.163 (0.14)	0.188 (0.15)	0.102 (0.09)
11	15	Managed Steep	0.075 (0.06)	0.049 (0.04)	0.094 (0.07)
11	15	Managed Flat	0.079 (0.07)	0.080 (0.07)	0.078 (0.07)
11	15	Natural Flat	0.079 (0.07)	0.089 (0.07)	0.043 (0.04)
11	15	Natural Steep	0.076 (0.07)	0.096 (0.08)	0.050 (0.04)
12	96	Managed Steep	0.451 (0.34)	0.301 (0.26)	0.551 (0.46)
12	96	Managed Flat	0.480 (0.41)	0.508 (0.44)	0.504 (0.43)
12	96	Natural Flat	0.472 (0.40)	0.536 (0.46)	0.299 (0.25)
12	96	Natural Steep	0.489 (0.43)	0.586 (0.48)	0.318 (0.26)
13	55	Managed Steep	0.195 (0.16)	0.118 (0.10)	0.225 (0.18)
13	55	Managed Flat	0.192 (0.17)	0.182 (0.16)	0.190 (0.16)
13	55	Natural Flat	0.190 (0.16)	0.207 (0.18)	0.109 (0.09)
13	55	Natural Steep	0.194 (0.17)	0.226 (0.19)	0.122 (0.10)
14	60	Managed Steep	0.199 (0.16)	0.122 (0.11)	0.230 (0.18)
14	60	Managed Flat	0.196 (0.17)	0.187 (0.16)	0.192 (0.16)
14	60	Natural Flat	0.193 (0.16)	0.214 (0.18)	0.112 (0.10)
14	60	Natural Steep	0.197 (0.17)	0.230 (0.19)	0.123 (0.10)
15	45	Managed Steep	0.162 (0.13)	0.099 (0.09)	0.190 (0.15)
15	45	Managed Flat	0.161 (0.14)	0.152 (0.13)	0.159 (0.14)
15	45	Natural Flat	0.158 (0.14)	0.173 (0.15)	0.092 (0.08)
15	45	Natural Steep	0.163 (0.15)	0.189 (0.16)	0.102 (0.09)
16	60	Managed Steep	0.199 (0.16)	0.123 (0.11)	0.230 (0.18)
16	60	Managed Flat	0.197 (0.17)	0.187 (0.16)	0.192 (0.17)
16	60	Natural Flat	0.193 (0.17)	0.211 (0.18)	0.112 (0.10)
16	60	Natural Steep	0.196 (0.17)	0.231 (0.19)	0.123 (0.10)
17	44	Managed Steep	0.161 (0.13)	0.099 (0.09)	0.182 (0.14)
17	44	Managed Flat	0.161 (0.14)	0.160 (0.14)	0.159 (0.14)
17	44	Natural Flat	0.158 (0.14)	0.180 (0.15)	0.092 (0.08)
17	44	Natural Steep	0.164 (0.15)	0.190 (0.15)	0.103 (0.09)
18	16	Managed Steep	0.074 (0.06)	0.049 (0.04)	0.093 (0.07)
18	16	Managed Flat	0.078 (0.07)	0.078 (0.07)	0.076 (0.07)
18	16	Natural Flat	0.078 (0.07)	0.088 (0.07)	0.042 (0.04)
18	16	Natural Steep	0.075 (0.07)	0.095 (0.08)	0.050 (0.04)

Values are means with standard deviation in parentheses.

Chapter 5: Synopsis & Outlook

In this thesis, considerable effort has been put into understanding the processes governing plant community structure and resulting functioning in agricultural field margins. This was done by focusing on describing naturally occurring plant communities of the field margins in the agricultural landscape of Haean-myun catchment in South Korea (Chapter 2) and how it can affect the ecosystem functioning (e.g. soil stability, soil erosion control) (Chapters 3 and 4), which consequently will help us to understand the functional role of the field margins as an important component of the agro-ecosystem.

With these premises let me in the following pages summarize and guide through the essence of the thesis, including summary of the key results, a general discussion on the importance of the thesis's findings, the future trends and some concluding remarks.

5.1 Summary

5.1.1 Effect of local-management and landscape-scale land-use on plant communities (Chapter 2)

Changes in land-use practices within agricultural landscapes, such as agriculture intensification and widespread removal of natural vegetation, have led to a decline in biodiversity (Fritch *et al.*, 2011). Diversity in agricultural landscapes is important for the conservation of typical cultural landscapes (Berkes & Davidson-Hunt, 2006; Gao *et al.*, 2013) and their species (Myers *et al.*, 2000; Pimm *et al.*, 2014) but also for ecosystem services such as pest control (Naeem *et al.*, 2012; Reich *et al.*, 2012). However, although a decline of biodiversity in response to land-use changes is well documented (Chapin *et al.*, 2000; Sala *et al.*, 2000) it often remains unclear which types of land management affect which components of biodiversity.

We study field margins in an agricultural landscape in South Korea. The area is subjected to rapid change in land-use, as it has been shifting over the last 40 years towards intensive agriculture, which led to an expansion in farm fields and a reduction in natural areas and (Kettering *et al.*, 2012). Within these agricultural landscapes, field margins have an important function for conservation (Marshall, 1988; Moonen & Marshall, 2001), as they provide species refuges as well as feeding and breeding habitats (Ma *et al.*, 2013). Field margins and their diversity also play an important function within the agroecosystem as they promote, for example, soil stability (Pohl *et al.*, 2009; Pérès *et al.*, 2013). In order to reduce species loss and the loss of important ecosystem functions, it is important to understand the effects of different aspects of land management, e.g. local field margin management and landscape structure, on the species growing within the field margins. In the studied field margins we contrast two main types of management. First, local management, which includes cutting, spraying herbicides to remove field margin vegetation, and deciding on field margin width. Second, the landscape-scale land-use management, which can affect the regional species pool and provides opportunities for species dispersal, is here measured as the percentage of non-farmed habitat.

To test how the local management and the landscape-scale land-use influence plant communities of agricultural field margins, we studied multi-facet plant community structure which includes alpha, beta and gamma diversities and species level characteristics such as rareness, growth forms and dispersal types. Firstly, we surveyed 100 field margins covering Haean-myun catchment. In each plot we measured four environmental variables: exposure, slope, width of the field margin and management type (i.e. "managed" for field margins that had signs of management activities from the ongoing season such as cutting or spraying herbicides and "unmanaged" for field margins that had left untouched in the season). For the botanical survey each plot was sampled using three subplots of one square meter per subplot; subplots were 4 m apart from each other. In each subplot, we estimated three different vegetation characteristics: vegetation cover (i.e. the percentage of ground covered by vegetation), species richness (i.e. the number of observed species) and species abundance (i.e. the number of observed individual / species). The managed field margins were sampled after one month of the management activities. Secondly, we classified all species into dispersal groups of either abiotic (wind- or unassisted dispersal) or biotic dispersal (e.g. by insects, birds, and mammals) and according to their growth form into annual and perennial according to Kim, M *et al.* (2000). Finally, to test the influence of the landscape-scale land-use, we calculated the percentage of the non-farmed habitats around each plot in five distinct buffer zones of 100, 200, 300, 400 and 500 m radii. Non-farmed habitats included field margins, fallows, forest, riparian areas, pasture and grassland in the land-use maps for 2010 provided by Seo *et al.* (2014).

To achieve our goal, we performed our data analyses in three steps: First, we calculated alpha (α) diversity of the 300 subplots, pairwise beta (β) diversity of the 100 plots, each represented by the mean species abundance in the three subplots, and, separately for the managed and unmanaged plots, gamma (γ) diversity. Second, we analyzed the effects of local management and landscape-scale land-use on alpha diversity using linear mixed effects models and on pairwise beta diversity by calculating local contribution to beta diversity (LCBD). Finally, we analyzed the species abundance response to local management and landscape-scale land-use using generalized linear mixed models.

Our results showed that the local management and landscape-scale land-use have very different effects, as local management influences mostly the more rare species, those with abiotic dispersal and with perennial growth form. In contrast, landscape-scale land-use influences more the abundance of species in the managed plots where the abundant species are perennials. Based on the species abundance, the managed field margins found to harbor fewer species and have a positive relation to landscape-scale land-use.

In conclusion, we emphasize the importance of the multi-scale approach as it supports an enriched and coherent portrayal of biodiversity responses to local and landscape-scale managements. As the local management is mainly affecting the plots that have no surrounding habitats, it is important that if the field margins are managed they should at least have access to non-farmed habitats in the surroundings to help increasing the plant diversity via species dispersal.

5.1.2 Effect of plant functional traits on soil stability (Chapter 3)

Soil stability is a key ecosystem function provided by agricultural landscapes, which refers to the ecosystem function of resistance to disintegration when disturbed. Soil stability is critical for water infiltration, root growth and resistance to water and wind erosion (Bronick & Lal, 2005; Gyssels *et al.*, 2005) and thus is a crucial soil property affecting soil sustainability and crop production (Letey, 1985). Soil stability can be measured in the field by several methods. The most common methods are: (1) Soil aggregate stability, which reflects how the soil aggregates react to precipitation, as the unstable aggregates tend to produce a slaked soil layer when it gets wet, which causes limitation in the infiltration rate, increasing the surface runoff and limiting the plant growth (Tisdall & Oades, 1982). (2) Soil penetration resistance, a composite soil property that is governed by more basic properties, including soil cohesion, soil compressibility and soil/metal friction (Dexter *et al.*, 2007). Penetration resistance correlates with several other important variables, such as root elongation rate (Taylor & Ratliff, 1969). (3) Soil shear vane strength, which measures the soil cohesiveness and resistance to shearing forces exerted by gravity, moving fluids and mechanical loads (Morgan, 2009). It reflects how the soil-root matrix produces a type of reinforced earth, which is much stronger than the soil or the roots separately and how this matrix can resist the environmental factors and human activities (Simon & Collison, 2001). There are many factors that control soil stability via direct and indirect pathways. Particularly important are abiotic soil characteristics such as soil texture and clay content (Denef & Six, 2005; Chenu *et al.*, 2011), biotic vegetation characteristics such as species richness, vegetation cover and plant diversity (Pohl *et al.*, 2009; Pérès *et al.*, 2013), and biotic functional characteristics such as plant roots, soil fauna, and microorganisms (Gyssels *et al.*, 2005).

To test the influence of vegetation characteristics (vegetation cover %, species richness and root density), soil characteristics (soil texture "silt and clay %") and plant functional traits (PFTs) on soil stability, we built a conceptual path model to disentangle these effects on soil aggregate stability, soil penetration resistance and soil shear vane strength. Using data collected from the field margins in Haean-myun catchment in Korea using 30 sampling plots of 1 m^2 (Fig. 5.1). In each plot (1) we estimated three different variables describing the vegetation characteristics; vegetation cover (i.e. the percentage of ground covered by vegetation), species richness (i.e. the number of observed species) and root density (estimated as percentage using a 30 cm x 30 cm metallic frame placed on the soil profile; (2) we measured above- and belowground PFTs for a total of 15 individuals of the 10 most representative species in the study site, these PFTs included plant height and leaf size for the aboveground compartment of each individual, root horizontal width (RHW), root length (RL), root diameter (RD), root dry mass (RDM), specific root length (SRL) and root/shoot ratio (RSR) as belowground traits. We then up-scaled the functional properties to the community level using community weighted means (CWM) for each of the PFTs based on ignoring or accounting for intraspecific trait variability (ITV). (3) We used bulk density, water content, wettability, percentage of clay and silt as soil characteristics at each of our 30 sampling plots. Before running the path model, we did variable selection based on a redundancy analysis (RDA), which allowed us to choose those variables and traits that showed a significant relation to soil stability. In a second step, we fitted the conceptual path model with all remaining variables based on a Partial Least Squares Path Modeling (PLS-PM) approach, separately for each of the stability measure with and without the ITV. Model evaluation of PLS-PMs was based on the R^2 coefficient for the soil stability measure and the overall model goodness-of-fit (GoF) index.

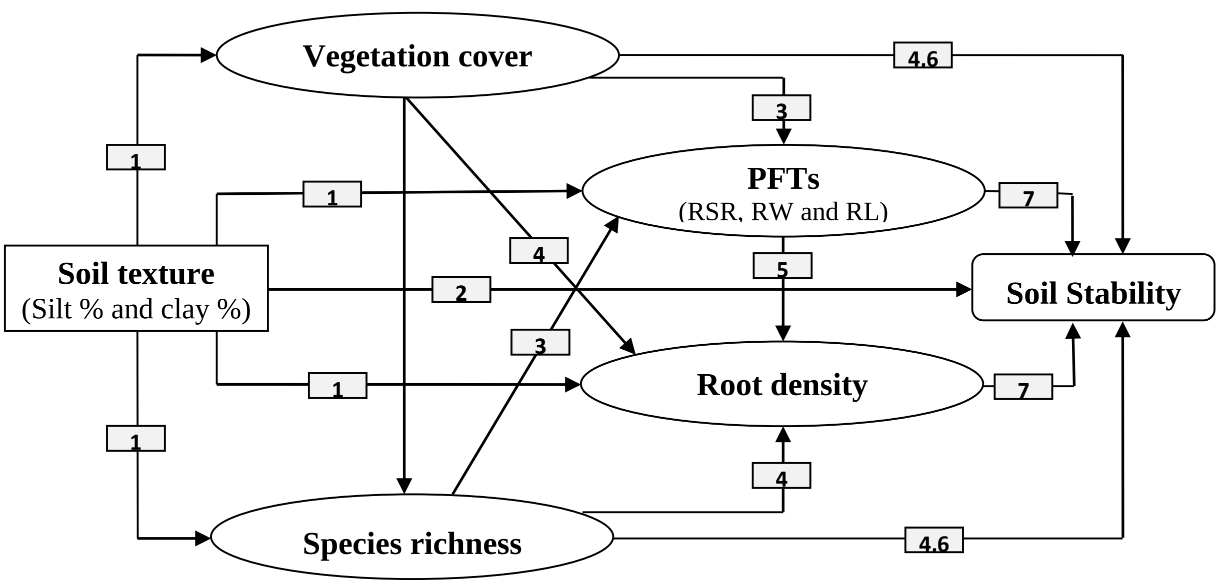

Fig. 5.1. A conceptual path model for effects of the abiotic soil characteristics (soil texture "silt % and clay %"), vegetation characteristics (vegetation cover, species richness and root density) and PFTs (RSR = root/shoot ratio, RL = root length and RW = root horizontal width) on three soil stability measures (Soil aggregate stability, soil penetration resistance and soil shear vane strength). Numbers on arrows indicate previous studies that support the path; 1. Lane *et al.* (1998), 2. Denef and Six (2005), 3. Petchey and Gaston (2002), 4. Pohl *et al.* (2009), 5. Reich *et al.* (2012), 6. Pérès *et al.* (2013) and 7. Gyssels *et al.* (2005).

Our results showed that soil stability is not only strongly influenced by abiotic variables (e.g. soil structure) and vegetation structure (e.g. cover and species richness) but also by the functional composition of plant communities. Furthermore, our results showed that ignoring intraspecific trait variability resulted in lower fit for our conceptual model to the data. Accounting for intraspecific variability, the three components of soil stability were either moderately (soil shear vane strength, soil penetration resistance) or well (soil aggregate stability) explained by our conceptual path model. In all three analyses, root density had the strongest direct effect on soil stability. Accounting in addition for indirect effects, we could show that PFTs had a similarly strong influence, which was mostly mediated by root density. The most important PFTs were root length and the root/shoot ratio. PFTs themselves were strongly affected by species richness and soil texture.

In conclusion, this study demonstrated the important role of intraspecific trait variability not only in responses of plant communities to changing conditions but also in their effect on key ecosystem functions. Results corroborate for an important specific example (soil stability in agricultural landscapes) earlier findings suggesting that the functional trait composition of communities can be much more important for ecosystem functioning than vegetation cover or species richness. These findings have important implications for managing field margins in order to improve soil stability as communities should not only be enriched by species with favorable root traits but it should also be considered that species show important plasticity in their root traits.

5.1.3 Effect of management and slope of field margin on soil erosion control (Chapter 4)

Soil erosion is one of the common problems affecting agricultural landscapes, especially in areas subjected to intensive rainfall events. Soil erosion has been intensifying in recent years (Pimentel *et al.*, 1995), and causes reductions in productivity, reaching 50% in some lands (Eswaran *et al.*, 2001). As mentioned before, field margins have a series of extremely important roles within the landscape, e.g. reflecting agricultural, environmental, conservation, recreational, and cultural or historical interests (Greaves & Marshall, 1987; Marshall & Moonen, 2002; Hickey & Doran, 2004; Olson & Wäckers, 2007; D'Acunto *et al.*, 2014). In this study we are concentrating on the field margin's environmental role in erosion control due to its efficiency in sediment trapping. As the vegetation of the field margin efficiently can trap sediment and protect soil against erosion by reducing runoff and by increasing infiltration rate into soil. One of the factors that influence soil erosion and runoff is slope steepness. It has been shown that erosion is expected to increase as a function of slope steepness (Zheng, 2006; Fu *et al.*, 2011), but this effect is also affected by other factors like soil properties (Singer & Blackard, 1982), surface conditions (Martínez *et al.*, 2006) and vegetation cover (Singer & Blackard, 1982; Hancock *et al.*, 2015).

To test the effect of management ("intensively managed", hereafter "managed" or "extensively managed", hereafter "natural") and slope degree ("steep" or "flat") of the field margin in erosion control, 12 sites were installed in Haean-myun catchment for our four different combinations, which are "managed-flat", "managed-steep", "natural-flat" and "natural-steep" with three replicates for each treatment (Fig. 1.3D).

Managed field margins were continuously managed by cutting for the whole season, while the natural ones were left without any type of management. Steep slopes were selected to have approximately a 35^{o} slope, while the flat slopes ranged from 1^{o} to 2^{o}. To reduce potential confounding factors other than management and slope, all sites were selected to be next to radish fields, which are considered to have the highest average annual soil erosion rate within our study catchment (Arnhold *et al.*, 2014), with the same age and field slope degree from 2^{o} to 5^{o}.

To trap the sediment that reached the field margins, Astroturf mats with a size of 34 cm x 25 cm (850 cm^2) (for more details see (Lambert & Walling, 1987; Walling & Owens, 2003), were installed at three levels: upslope, immediately before the field margin to quantify the sediments that reach it, in the middle of the field margin to quantify the locally trapped sediments, and after the field margin at the downslope edge to quantify the sediments that leave the field margin to the next field or to the stream. In total, 15 mats were installed at each site, with five mats at each level (Fig. 5.2). Mats were installed in May 2013 and were monitored after each rain event until the end of the monsoon season. Mats containing sediments were collected and transferred to the laboratory, where the sediments were dried at room temperature, removed from the mats and weighed.

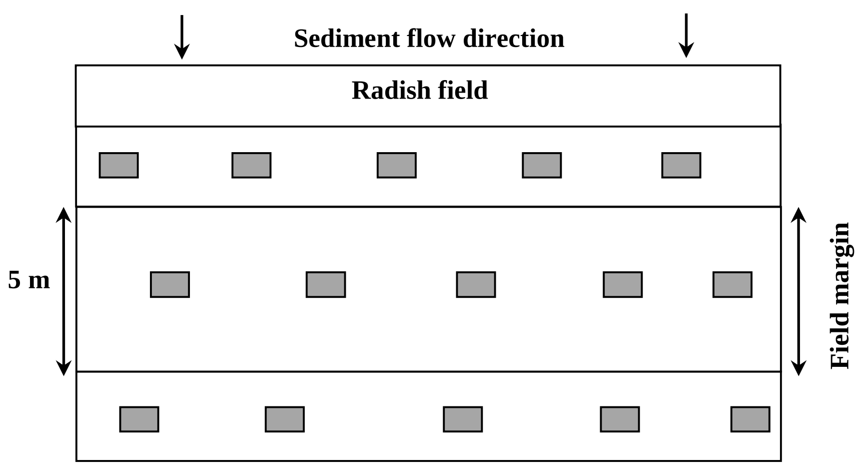

Fig. 5.2. Schematic diagram showing the location of the Astroturf mats (grey squares) before, within and after the field margin. All the field margins selected to have the width of 5 m and to be next to radish fields.

Our results showed that in all cases, there is a positive relation between rainfall and sediment collected. Natural field margins showed high efficiency in reducing soil erosion in comparison to the managed ones. For the field margin slope, it showed effectiveness in combination with vegetation cover, as natural margins that have steep slopes had more sediment trapped in comparison to the managed margins.

In conclusion, this study demonstrated the important role of field margins in controlling water soil erosion in agricultural landscapes, especially those which face huge rainfall amounts. These findings have important implications for field margins’ management, placement and design within the agricultural landscape in order to effectively control soil erosion.

5.2 Outlook

The plant communities of field margins are an important aspect of agroecosystem ecology. A major research challenge was to link studies aiming to understand the determinants of species distribution on the one hand and the consequences of biodiversity patterns for ecosystem functioning on the other hand.

Study of the drivers of multi-scale plant community structure in agricultural field margins revealed a better understanding of the effects of local field margins’ management on plant communities and how it can affect important ecosystem services in agricultural landscapes. There is still scope for further research in this area, as the possibility of testing the effect of local management and landscape context on the functional composition of plant communities needs more research.

The next chapter describes the effect of the functional composition of plant communities on soil stability as one of the important ecosystem services in agricultural landscapes that face monsoonal climate. The value of the results from this study could be increased further by more applied research about the functional roles of the plant communities and how it can affect the whole ecosystem. Thus, testing the functional role of plant communities should not be restricted to experimental fields but in addition more field work in different geographic areas with different climatic conditions would allow for a better assessment of the functionality of field margins. While the results of this study point towards functionality of field margins in areas facing monsoonal climate, more research on different ecosystem functioning (e.g. nutrient cycling) would be beneficial.

Results of the erosion control using field margins showed how effective the field margins' vegetation in mitigating soil erosion is. Further work is needed to mitigate soil erosion in agriculture landscapes using field margins. To achieve this goal, it is important to investigate the source and pathways by which sediment are transported to waterbodies on a catchment scale, which can be done using models, tracers and field experiments. Furthermore, socio-economic studies on the costs and benefits of having wider field margins, which can lead to flatter slopes, should be conducted; this should be done via interacting with the farmers to focus the work and promote findings. Finally, a robust field margin management plan should be developed in Korea to provide a dense vegetation cover to prevent soil erosion.

5.2.1 Future plan for field margin placement and design:

Due to the importance of the field margins in soil erosion control within the agricultural landscapes, a decision support system (DSS) framework has been implemented by Deeks *et al.* (2012), for the effective design and placement of the vegetated field margins within the agricultural field system in the UK. We have found that most of the research on effectiveness of field margins in controlling soil erosion were conducted in the UK to test the capability of field margins to trap sediment and the associated nutrients (Owens *et al.*, 2007) or to apply erosion models for the assessment of field margin performance in erosion control (Duzant *et al.*, 2010). On the other hand, we didn't find any research that has been done in areas with monsoon climate like South Korean agricultural landscapes. A step forward from these studies that have been done in the UK, our results showed how the management activities and slope degree of field margins are of a great importance in soil erosion control. This will help in providing local farmers with specific guidelines for managing field margins to get the maximum benefits out of them in areas like South Korean agricultural landscapes, which are characterized by a monsoon climate.

Based on the results of the current study, previous studies which have been done in Haean-myun catchment, and the DSS framework, we feel that several adjustments to field margins in areas that have monsoonal climate are profitable, which can be explained in six main steps as follows (Fig. 5.3):

1. Identify fields with soil erosion problems: in this step, target fields that have high risk of erosion are identified, which we can achieve by local knowledge, soil erosion models, and farm advisors (Arnhold *et al.*, 2013; Arnhold *et al.*, 2014).
2. Identify sediment flow pathways and target location of the field margin features: in order to achieve this step, we have to identify the flow direction of the sediment and the field margin positions, which can be done using adding local information about erosion to a topographic map, or by using erosion models.
3. Identify methods to prevent or reduce soil erosion: after identifying the sites that susceptible to erosion risk, we will propose the best method to prevent soil erosion, which can be done based on our current results by considering increasing the vegetation cover and reducing the vegetation removal by cutting or spraying herbicides, especially within the field margins that have steep slopes.
4. Consider the proper width of field margin: Here we are considering the field margin's design; according to Yuan *et al.* (2009), the effective width of field margins should range between three and six meters as it can remove fair amounts of sediments.
5. Field margin establishment and vegetation cover: once we have selected the field margins and its design, we have to check three important features (1) the field margin's width, which should be in the range that helps controlling erosion; (2) the field margin's slope, if it is steep or flat and (3) the vegetation cover percentage which will depend on the field margin's slope and width.

6. Field margin monitoring: as a guarantee that the field margins are functionally controlling the soil erosion, it should be monitored frequently to check for any changes that may make it less functional, which can include (1) gaps that may appear within the field margin due to sediment flow; (2) soil compaction, which can appear due to human and animal movement and will affect infiltration rate and sediment deposition and (3) vegetation cover reduction, due to grazing, soil compaction, age or diseases (Owens *et al.*, 2007; Deeks *et al.*, 2012).

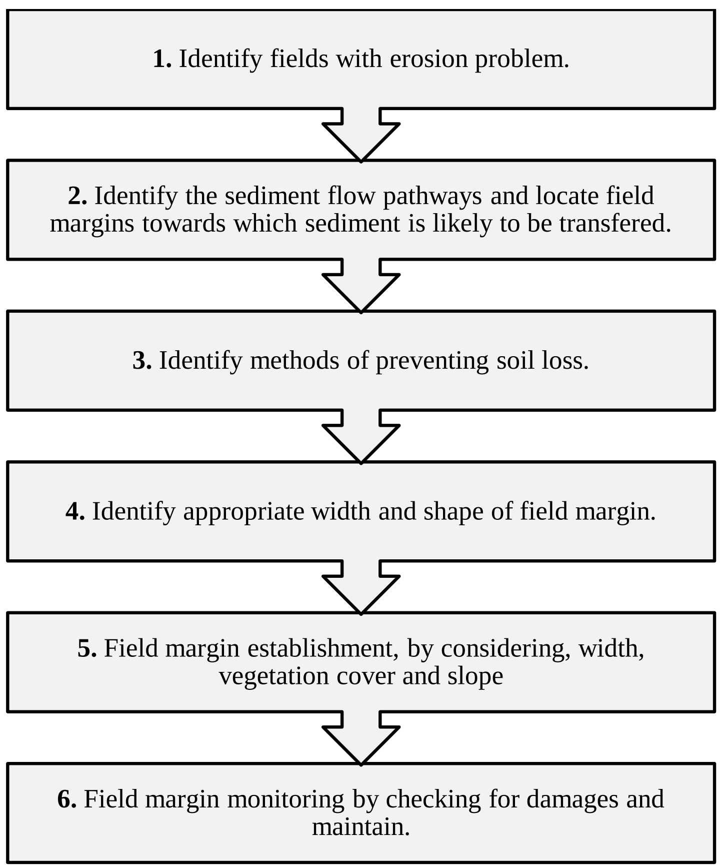

Fig. 5.3. Schematic diagram of our future plan for functional placement and design of field margins within agriculture landscape to reduce soil erosion (modified after Deeks et al. (2012)).

5.3 Concluding remarks

As agricultural landscapes occupying around 50% of the earth's land surface (USDA, 2013), it is pivotal to sustain and maintain the biodiversity in these system to improve the ecosystem functioning. In this thesis, we provided several recommendations for improving the ecosystem functions in agricultural landscapes using the field margins as a functional component of the agroecosystem (Fig. 1.1).

We showed how important the local-management of the field margins and the surrounding landscape-scale land-use in maintaining the diversity in the agricultural landscapes. For areas like South Korea, better laws and strategies should be developed to control the field margin's local management, which will help in conserving the biodiversity by providing the suitable habitats for flora and fauna and consequently, will affect the soil quality and stability which will help in controlling the soil erosion happens during the monsoon time in South Korea. Furthermore, we demonstrated how essential is the field margin's plant functional community composition on soil stability as an important ecosystem function in the agricultural landscapes. Finally, we modified a pre-existing future decision support system (DSS) framework for the effective design and placement of the vegetated field margins within the agricultural field system to help in protecting soil erosion via field margins in agricultural landscapes that face monsoonal climate.

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