UNIVERSIDAD NACIONAL DE COLOMBIA

Efecto de los remanentes de bosques nativos sobre el control biológico y la productividad en cultivos tradicionales de maíz (*Zea mays* L.)

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Resumen

La expansión de la frontera agrícola es una de las principales causas de pérdida de la biodiversidad y detrimento de las funciones ecosistémicas esenciales para la producción agrícola, entre ellas el control biológico de plagas. En este trabajo, se evaluaron las relaciones entre la pérdida de cobertura de los bosques nativos, la diversidad de arvenses y artrópodos dentro de los cultivos y su relación con la herbivoría y la producción en doce cultivos tradicionales de maíz en Topaipí (Cundinamarca), durante la segunda temporada de siembra de 2011.

En los cultivos estudiados el control biológico de plagas fue proporcionado por predadores y parasitoides nativos, y estos a su vez dependieron del mantenimiento de la diversidad de arvenses dentro de los cultivos. La cobertura de bosques promovió la complejidad de las redes de interacción plantas-artrópodos en este sistema, en los que la riqueza de depredadores se asoció con una mayor producción de los cultivos. Por lo anterior, la conservación de los bosques en sistemas de cultivos tradicionales es esencial para el control biológico, la producción y la conservación de la biodiversidad.

Palabras clave: agrobiodiversidad, cobertura de bosque, control biológico, cultivos tradicionales, herbivoría, pérdida de hábitats, redes de interacción plantas-artrópodos, *Zea mays* L.

Abstract

The expansion of the agricultural frontier is one of the main causes of biodiversity loss and detriment of ecosystem services essential for agricultural production, including biological pest control. In this work, the relationship between the loss of native forest cover, diversity of arthropods and weeds in crops and its relationship with herbivory and crop production was examined, using twelve traditional corn crop fields in Topaipí (Cundinamarca) during the second growing season in 2011.

In the studied cornfields pest control was provided by native predators and parasitoids, which in turn depended upon the maintenance of the diversity of weeds within crops. Forest cover promoted complexity of networks of plant-arthropod in this system, in which the richness of predators was associated with increased production of crops. Therefore, the conservation of forests in traditional crop systems is essential for biological control, production and biodiversity conservation.

Keywords: agrobiodiversity, pest control, herbivory, habitat loss, interaction networks, traditional crop systems, *Zea mays* L.

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Introduction

This work considers the impacts of landscape simplification on biodiversity, herbivory and production in traditional Andean cornfields. Forest conversion for agriculture reached 69% by 1998 in the Colombian Andean region (Etter *et al.* 2006), leading to more simplified landscapes currently dominated by agricultural areas. Previous work in highland Andean agroecosystems has shown that landscape simplification reduces the richness and abundance of herbivores and their natural enemies in crops, whereas increases pest pressure on crops (Poveda *et al.* 2012). However, in most cases the effect of natural habitats on diversity has been evaluated for arthropods at local spatial scales, in temperate regions (Bianchi *et al.* 2006, Chaplin-Kramer *et al.* 2011, Shackelford *et al.* 2013). Little is known about their effect on more complex crop systems, such as tropical indigenous crop systems that, besides arthropods, also maintain a high diversity of weeds. Furthermore, agricultural fields are also highly disturbed and homogenization of communities can occur through dominance of superior competitors and loss of rare species.Therefore, to conserve diversity and to develop more sustainable pest management strategies, we must understand the factors that influence patterns of species distribution and abundance in human-dominated landscapes.

This work addressed basic research in Agroecolgy. First, results provide insight into the ecological mechanisms that explain why diversity and resilience to pest attack are higher in traditional crops than in conventional ones. Second, this work allows us to explore the role of biodiversity in specific ecosystem functions, such as herbivory, pest control and food production. And third, studying the role of native forest on agricultural biodiversity is relevant to reduce the trade-off between increasing food production and conservation of biodiversity and its associated ecosystem services, a major challenge for agriculture in the twenty-one century (Pretty *et al.* 2010).

This work also contributes to the knowledge of the ecological structure of the tropical agroecosystems, an issue poorly described until now, because of the reluctance of ecologists for studying patterns of diversity in agroecosystems. Besides classical descriptor of communities, such as species richness and diversity indexes, here I describe patterns in networks of species interactions, patterns in relative abundance of species and dominance, differences in species composition among the cornfields related to the presence of forest around the fields and patterns of meta-community level. Because these ecological patterns are frequently related to ecological processes, the results provide a useful tool to connect biodiversity and ecological processes with the agronomic characteristics of the farms and the provision of ecosystem services in human-dominated landscapes. These findings may contribute to develop generalizations about the mechanisms that explain why traditional crop systems conserve high diversity and maintain several ecological functions at the same time.

To address these issues, I studied the relationships between the presence of native forest and the diversity of within crop weeds and arthropods, as well as their relationships with herbivory and production in traditional cornfields in the Colombian Andes, during the second growing season in 2011.

I examine several predictions about the impact of native forest on biodiversity of weeds and arhtropods, herbivory and crop yield: First, as native forest is a permanent habitat in the agricultural landscape where populations of arthropods may build up longer without disturbance, I hypothesize that the amount of native forest around each cornfield will be associated with a higher diversity of arthropods within the fields, and with a more complex structure of ecological networks of plant-arthropod interactions. Second, I expect a positive relationship between the amount of native forest around the cornfield and the abundance and diversity of pest's natural enemies, which in turn will translate into a better pest regulation in crops. Thus, I expect that the more forest around the crops, the less damage inflicted by herbivores to the crop and the higher the crop yield. Third, I expect a low turnover of species among the cornfields, with the same dominant species in most of the cornfields. That might happen because of the relative small area covered by the study, so dispersal limitation is not likely to occur for most mobile taxa. In addition, land preparation for sowing leads to a relative "homogeneity" of all fields on the initial stage of the crop. And fourth, as vertebrate populations are highly dependent on the availability of forest for different resources, I expect that their role in the crops will increase as the cover of forest around the crop also increases. I expect that the role of vertebrates as natural enemies of insect pest populations will be greater than their role as herbivores in cornfields.

I tested these hypotheses by selecting twelve traditional cornfields in an area of $14km^2$. The cornfields were located in a gradient of forest coverage within a radius of 250 m around on them. I also evaluated the effects of other covariates deemed of importance, including soil organic matter, field former land-use, altitude and perimeter--area-ratio of each field. Using such a system I addressed the following questions:

- How does alpha biodiversity in cornfields change across a gradient of forest cover and other environmental factors for different taxa in this area?
- To what extent beta diversity changes among different taxa and among rare and common species?
- Which environmental factors are related to differences in species composition among cornfields?
- How does species composition and relative abundance of species change between cornfields?
- How does the structure of weed-arthropods assemblages change across a gradient of forest cover and other environmental factors?
- To what extent are herbivory and crop yield affected by the amount of native forest and the biodiversity associated with corn crops?
- What is the relative contribution of vertebrates to herbivory and pest control in traditional cornfields?

Beyond the scientific results, this information should be useful for decision-makers to define policy such as payments for ecosystem services to small landholders who produce food in a sustainable way, and also as baseline for pest management programs based on habitat manipulation, where native plant diversity can be used in strategies such as trap plants and repellent plants for pest, as well as in conservational pest control.

1. Conceptual framework

The development of a new model of sustainable agriculture is a major challenge in Agroecology (Altieri 1991, Prager *et al.* 2002, Gliessman 2007, Gliessman 2010, Vandermeer 2011, Altieri and Nicholls 2012). Indeed, it has been proposed that agro-ecological technologies can be developed to tackle the environmental degradation, food insecurity and social inequity created by the current food system –the global network of food production, distribution, and food consumption– (Gliessman 2007, Gliessman 2010, Altieri and Nicholls 2012). Some authors have argued that to cope with the growing demand for food, as well as, for agricultural land, it is necessary not only to expand the agricultural frontier, but also to intensify food production with ecologic-based technologies (Tilman *et al.* 2011, Cunningham *et al.* 2013).

In such context, the ecological functions provided by biodiversity play a central role in achieving “a sustainable intensification of agriculture” (Pretty 2008). However, more research is warrant to understand: *i)* the impacts of habitat loss on biodiversity, *ii)* how biodiversity affects ecological functions, and *iii)* how such functions generate ecosystem services (Fig. 1).

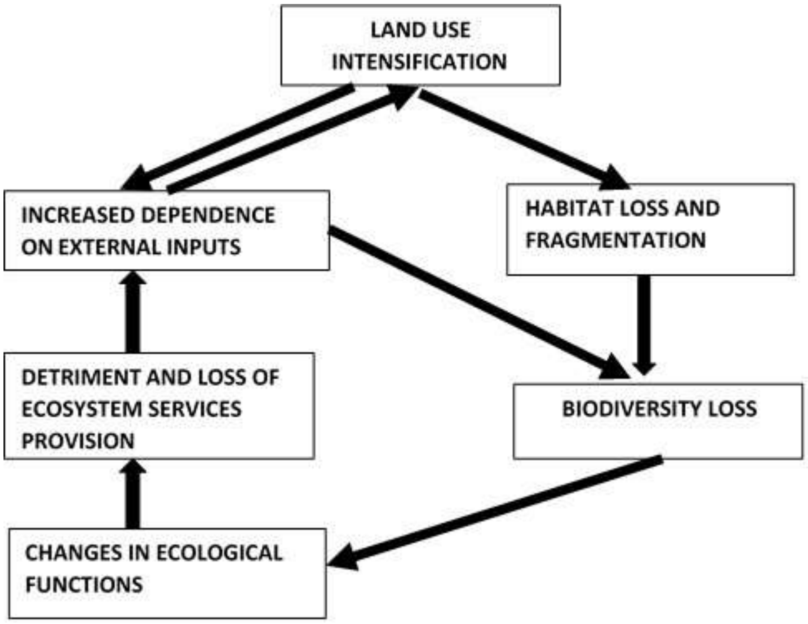

Figure 1-1. Conceptual framework showing the core concepts addressed by this work and its relationships.

1.1 Challenges for sustainable agriculture

Currently, almost 40% of the Earth's continental surface is covered by croplands and pastures. As agriculture and grazing expand, natural habitats have been reduced and fragmented and loss of species is occurring at the highest rate observed in the geological history of the Earth (Dirzo and Raven 2003). Poor management practices of modern agriculture are leading to degradation of agroecosystems with a negative effect on natural resources ("natural capital") that sustain life and human well-being in the planet (Daily 1997). For instance, soils become more vulnerable to wind and water erosion because of practices such as elimination of vegetative cover, excessive mechanization and tillage, whereas in other areas land productivity is being destroyed by flood irrigation, which is leading to soil salinization (Hillel and Rosenweigz 2008). In addition, the adoption of high-yielding crop varieties is leading to biological uniformity by eliminating the diversity of local or traditional crop varieties (Brush 1992).

The dependence of agriculture on external inputs has also increased. For example, worldwide consumption of nitrogenous fertilizers has increased from 10.8 million tons to 85.1 tons from 1960 to 2003 (MEA 2005), whereas the average annual worldwide consumption of pesticides was 292.050 tons between 1990 and 2010 (www.faostat.fao.org). Higher use of pesticides is prompted by landscape simplification (Meehan *et al.* 2011), as well as by the constant application of pesticides, which enhances problems such as pest resurgence, secondary pest outbreaks and pesticide resistance -a process known as the "pesticide treadmill"- (Vandermeer 2011). These processes occur because pesticides kill the target pest, but also kill the nontarget natural enemies and some pests may able to "resurge" after the pesticide use, whereas some secondary pests may be released from natural predatory control causing secondary pest outbreaks (Vandermeer 2011). In addition, the development of pesticide resistance reduces the efficacy of chemical control increasing the demand for pesticides, e.g. by 1991, 504 arthropods had developed resistance to at least one insecticide (Georghiou and Lagunes-Tejada 1991)

Besides the detriment of biodiversity and ecosystem functioning, agriculture have to tackle some challenges imposed by human growth and global changes in climate and food trade. For instance, in the 21st century an increase in crop production by 70-100 per cent is needed to meet the growing demand for food, with only about 10 percent of land suitable for agriculture (Pretty et al 2010). Food production has to be adapted to climate change, which increases the probability of extreme climatic events such as droughts, floods and frosts. In addition, changes in policies are needed to achieve equity in the access to land and water for irrigation as well as to stop the decline in the number of units of small traditional and family farmers, who have been forced off their land and out of agriculture (Gliessman 2010). Only by considering together ecological, social and economic factors of food systems it is possible to overcome the hunger and malnutrition that currently affect almost 870 million of people worldwide (www.faostat.org)

In such a context, modern agriculture needs a transition towards sustainability. This sustainability refers to a model of agriculture that seeks to provide long-term sustained yield, using management technologies that integrate the components of the system in order to improve their biological efficiency and maintaining the productive capacity of the agroecosystem (Prager *et al.* 2002). At the same time, sustainable agriculture should have the capacity to buffer shocks and stresses (resilience) and the capacity to continue over long periods (Pretty 2008).

Agroecologists suggest that such transition towards sustainability should be done by designing agroecosystems that resemble as much as possible the functioning of natural ecosystems (Vandermeer 2011). Indeed, some ecological principles or commonalities have been drawn from studying sustainable traditional crop systems (Altieri 1991, Gliessman 2007 , Vandermeer 2011):

- A large number of species associated with them, not only of intentionally introduced or maintained specifically by the farmers with utilitarian purpose, but also of associated species which are naturally distributed in agroecosystems.
- Practice a low-input agriculture, relying mainly on human and animal energy and recycling within the farm.
- Nutrient recycling tends to be relatively closed. They integrate crops with animal production, thus animal wastes are recycled into the cropping system.
- They rely on traditional varieties of crops and animals
- Are adapted to local conditions, rather than dependent on massive alteration or control of the environment.
- Maximize yield without sacrificing the long term productive capacity of the entire system.

- Maintain the multifunctionality of agroecosystems, which means that food and fiber production is encompassed with other ecosystem services such as clean water provision, maintenance of soil fertility, and conservation of natural habitats, biodiversity and landscape quality.
- They are built on the knowledge and culture of local inhabitants.

These ecological principles can be used to design new, improved and sustainable agroecosystems (Altieri 1991). The intention is not to come back food production to traditional practices or translate them directly to regions dominated by modern agriculture (Gliessman 2007). However, these principles serve as general guidelines for the transformation of modern agriculture (Gliessman 2010).

1.2. Land use intensification and habitat loss

Modern agriculture based on external inputs and mechanization of soils has encouraged the specialization of entire regions to produce particular goods, as well as the conversion of natural habitats to intensive agricultural land (Firbank 2005). As a result, the diversity of habitats has declined and agricultural landscapes have become homogeneous (Firbank 2008).

The demand for agricultural crops is increasing and may continue to do so for decades (Tilman *et al.* 2011). Therefore, increasing food production will take place through both a more intensive use of existing croplands and increasing land clearing (Pretty *et al.* 2010, Tilman *et al.* 2011). A recent forecast of land clearing estimates that approximately one billion hectares of forest will be converted to croplands by 2050 if the actual trend of forest conversion is held (Tilman *et al.* 2011), and it is expectable that the highest rates of forest conversion occurs in Latin America (Tilman *et al.* 2001). In addition, most of the best quality farmland is already used for agriculture, thus the expansion of agriculture would occur on marginal land, that is unlikely to sustain high yields and is vulnerable to degradation (Tilman *et al.* 2002).

Such estimations about the impacts of agriculture on natural habitats increase the concern about the loss of biodiversity, since habitat loss and fragmentation are the major threats to biodiversity (Sala et al 2000, Dirzo & Raven 2003, Tscharntke et al 2005). To tackle the problem of deforestation growing rates in developing countries, it has been suggested that "raising yields on existing farmland is essential for saving land for nature" (Tilman *et al.* 2002). This assumption is based on the idea that if per unit production increase, the required land base would be reduced, more land will be available for conservation; however, as pointed by Vandermeer (2010) this argument is an "article of faith", and it is also probable that technological progress makes agriculture more profitable and gives farmers an incentive to expand production to additional land. Thus, there is no simple solution to slow down forest conversion into croplands, and economic and cultural factors should be taken into account to tackle this problem.

Intensification of agriculture through achievements in precision agriculture, as well as in breeding programs and biotechnology solutions that improve the efficiency of crop nitrogen, phosphorous and water use, have been proposed as possible solutions to meet the growing demand for food without compromising the natural resources (Tilman *et al.* 2001). However, translation of new innovations in plant sciences into concrete benefits for poor farmers had not occurred in the past decades of green revolution, and it will require incentives and funding mechanisms that promote technology transfer (Delmer 2005). On the other hand, focusing on increasing yield crops does not tackle the real causes of hunger and environmental degradation (Rosset *et al.* 2000), moreover, it is unlikely that the same technology that had destroyed the natural resources that support life and food production can solve its depletion and degradation. Thus, specific knowledge, technological innovations, and changes in policies are needed to cope with the fundamental conflict between the increasing needs of agriculture and the maintenance of non-crop biodiversity at present levels (Firbank *et al.* 2008).

Environmental policy elements should on the one hand encourage agricultural practices that maximize diversity instead of minimizing it and on the other hand favor restoration and continuity of high quality more-natural habitats as part of the agricultural mosaic (Fahrig *et al.* 2011a, Cunningham *et al.* 2013). Additionally, to balance agriculture and food production it is necessary to identify which part of the existing biota is living in cultivated or human occupied areas (Paoletti *et al.* 1992), and if such diversity can be used as a tool for improving ecosystem service provision and human well-being. Finally, because much of the diversity in agroecosystems may exist at scales beyond the farm (Swift *et al.* 2004), and dynamics of diversity operate at different spatial scales (Tscharntke *et al.* 2012), considering management strategies at the landscape level is necessary to meet the challenge of food demand while preserving natural resources.

The management of land use patterns is of great importance for the conservation of biodiversity (Walz 2011). Nevertheless, a miscellany of terms in the literature has been utilized to refer to landscape structure and its impact on biodiversity, such as landscape simplification, landscape complexity, landscape heterogeneity, fragmentation and habitat loss. Thus, it is necessary to clarify what are the landscape characteristics addressed by these terms before discussing their relationships with the biodiversity and the supply of ecosystem services.

Landscape structure refers to the pattern of landscape, which is determined by its type of use, as well as by the size, shape, arrangement and distribution of individual landscape elements (Walz 2011). Fragmentation is defined as the process of habitat breaking (Schüepp *et al.* 2011), reflecting aspects of habitat configuration modification, including number of habitat fragments, edge density, and patch shape (Swift and Hannon 2010). In addition, in fragmented landscapes, the distance to viable habitats or degree of isolation may determine patterns of diversity. Habitat loss refers to the entire quantity of habitat in a landscape and particularly to the decrease in its size across time and/or space (Schüepp *et al.* 2011). Landscape heterogeneity indicates the variability of the landscape's properties in spatial terms (Walz 2011), a more heterogeneous landscape is a landscape with a larger variety of different cover types (compositional heterogeneity) and/or a more complex spatial patterning of them (configurational heterogeneity) (Fahrig *et al.* 2011a). Landscape simplification indicates the transition from agricultural landscapes dominated by natural habitats to landscapes dominated by croplands (Meehan *et al.* 2011).

As summarized by Walz (2011), the quality of landscape structure can be assessed by indicators of use intensity and structural diversity: *i)* the surface areas of natural and seminatural habitats types in the landscape is used as a measure of human influence on a natural environment; *ii)* the number of habitats types per area unit indicates habitat diversity;

iii) the proportional area of arable land in the landscape estimates the level of agricultural intensification; and *iv)* the distance to a particular type of habitat or the total length of all roads outside of settlements indicates isolation or fragmentation of habitats.

1.3 Impacts of habitat transformation on biodiversity loss and ecosystem functioning

Habitat loss and fragmentation are the major causes of biodiversity loss (Tilman *et al.* 2001, Tilman *et al.* 2002, Dirzo and Raven 2003, Tscharntke *et al.* 2005a). Yet, not all species possess the same chance of being lost as a result of simplification of agroecosystems and even some species may be more tolerant to habitat loss than others (Tscharntke *et al.* 2012). Therefore, organism's responses to landscape changes are extremely dependent on the species' characteristics. For example, species with low reproductive rates are particularly sensitive to habitat loss or fragmentation, which suggests that these species suffer of a limited ability to respond to the effects of environmental disturbance (Swift & Hannon 2010). Species with greater emigration rates required more habitat for persistence, especially if mortality may be higher in the matrix than in habitat patches, due to such factors as predation and mortality from unfavorable physical conditions (Swift and Hannon 2010). Ultimately, increasing homogeneity of habitats causes loss of biodiversity if species associated with farmland cannot meet resources and habitat conditions required through their full life cycles (Firbank 2005).

Besides local extinctions, changes in landscape and land management may involve changes in distribution and abundance of species (Firbank 2005), as well as in the ecological responses of organisms, including animal movement, population persistence, species interactions and ecosystem function (Fahrig *et al.* 2011a). The movement of animals between habitat types in the agricultural landscape can be viewed in light of source-sink population dynamics: permanent and undisturbed habitats (e.g. forest, pasture, field margins and hedgerows), serve as a refuge and source habitats from which arthropods could recolonize crop fields following management practices (Thorbek and Bilde 2004). For example, forest patches in agricultural landscape can improve pollination and pest control with a positive effect on crop yields (Bodin *et al.* 2006). Otherwise, homogenization of habitats e.g. through expansion of monocultures, may facilitate the movement of invasive species and the introduction of a superior competitor of desirable species (Swift *et al.* 2004). For instance, increases in the size, density and connectivity of host crop patches are expected to facilitate movement and establishment of crop pests, leading to higher pest pressure regardless of natural enemy activity (Meehan et al 2011).

Loss of natural habitats is associated not only with changes in species richness and diversity of pollinators, but also with the pattern of species interactions that link them in networks and the functions that species perform (Gonzalez *et al.* 2011), with serious implications for yield crops, given that 35% of the crop production volume and 70% of major global crops rely on animal pollination (Klein *et al.* 2007). In addition, the simplification of the environment and a decrease in trophic interactions is leading to the lack of self-regulation of population of crop plants or animals in agroecosystems, increasing the risk of pest and disease outbreak, despite the intensive human interference (Gliessman 2007).

The accessibility of natural habitats in agricultural landscapes is critical for pest control. Empirical evidence suggests that natural and semi-natural habitats embedded in agroecosystems maintain the regional pool of species of beneficial arthropods (Schmidt *et al.* 2005, Schmidt and Tscharntke 2005, Klein *et al.* 2006, Pluess *et al.* 2010, Wanger *et al.* 2010, Chaplin-Kramer *et al.* 2011), whereas, isolation from forest, reduce the diversity of natural enemies in crops (Klein *et al.* 2006, Rand *et al.* 2006, Schüepp *et al.* 2011). Various mechanisms have been suggested to explain these relationships in addition to the source-sink population dynamic previously described. First, natural habitats are permanent covers, where beneficial arthropods can build-up larger populations without disturbance. Second, arthropods benefit from natural habitats because they can meet sufficient food resources, such as nectar, pollen and alternative preys that enhance their longevity or fecundity (Tylianakis *et al.* 2004, Lee and Heimpel 2008). And third, field boundaries provide not only foraging habitats, but also nesting places and maintain populations of pollinators (Hellwing and Frankl 2000) and predators in crops (Drapela *et al.* 2008, Pluess *et al.* 2010). Non-crop plants may favor natural enemies by supporting non-pest alternative hosts or prey, and also provide shelter or a moderate microclimate (Gurr *et al.* 2003a). However, plants may also benefit herbivores (Lavandero *et al.* 2006a) and thus increased plant diversity per se may not result in a better pest suppression.

Despite of the fact that the positive effect of local and landscape factors on the biodiversity of pollinator and natural enemies is well known, the mechanistic link between biodiversity and the provision of ecosystem services is still poorly understood (Shackelford *et al.* 2013). Given that most studies evaluate the impact of biodiversity on pest control using the abundance or the richness of a service provider as a proxy for ecosystem service (Shackelford *et al.* 2013) examples of direct measurements of pest control are scarce (Gardiner *et al.* 2009).

1.4. Links between biodiversity and ecosystem service provisioning

Land use intensification, through both land conversion and agronomic practices that increase yield crops, may affect the provision of ecosystem services via the loss of biodiversity (Tscharntke *et al.* 2005a, Gonzalez *et al.* 2011). Particularly, agriculture is affected by the disruption of communities of arthropods which are responsible for the provision of pollination and pest control, which are services highly vulnerable to land-use intensification in agroecosystems (Firbank *et al.* 2008, Flynn *et al.* 2009, Lindenmayer *et al.* 2012). For instance, in a review of the relationships among landscape composition, biodiversity and pest control (Bianchi *et al.* 2006) the authors reported that in 74% and 45% of the studies, natural enemy populations were higher and pest pressure lower in complex landscapes versus simple landscapes, suggesting that landscape simplification and the decline of biodiversity may affect the functioning of natural pest control. Likewise, in a review of landscape effects on crop pollination (Ricketts *et al.* 2008) the authors reported that crop visitation rates decline with increasing distance from pollinator habitats, suggesting that the declining on diversity of pollinator threatened the productivity, diversity and stability of food production systems. An economic assessment of pollination and pest control highlighted the importance of these services for agriculture, and estimated that both services are worth $8 billion to the United States agriculture each year (Losey and Vaughan 2006).

Particularly for pest control, the efficiency of biological control might depend on the diversity within trophic levels: a higher diversity within the natural enemies' trophic level may increase overall predator efficiency, via complementarity and sampling effects (Bohan *et al.* 2013). Therefore, biodiversity may enhance functioning when a diverse pool of species exploits the same resources in different ways (resource partitioning), thus each specie contributes to the function via a unique (complementary) occupation of the total niche (Tscharntke *et al.* 2005a). On the other hand "sampling effect" refers to higher probability of sampling species that have a higher potential contribution to the function in diverse species pool (Tscharntke *et al.* 2005a). Thus, positive effects of complementarity in pest control arise when natural enemies' had little overlap but significant segregation in host/prey use (e. g. Tscharntke et. al. 1992, Schmidt et al 2003, Cardinale 2003, Crowder et al 2010). However, competitive interactions among natural enemies, as well as, omnivory and intraguild predation may constrain pest control in diverse agroecosystems (Thies *et al.* 2005, Martin *et al.* 2013). In addition, a larger diversity of primary consumers may also dilute the action of natural enemy predators by providing alternative preys (Bohan *et al.* 2013).

Biodiversity also contributes to ecosystem functioning through redundancy in functional groups, which provides 'resilience' or the capacity of reorganization after disturbance (Tscharntke *et al.* 2005a). Such property is important in highly disturbed environments, in which spatial/temporal heterogeneity as well local extinctions are common. Thus, only diverse communities may support species that become important as soon as other disappear, which is known as "the insurance hypothesis" (Loreau et al 2003). For instance spatio-temporal variation in effectiveness of natural enemies has reported in aphid-enemy interactions, in which the importance of ground dwelling predators and parasitoids varied among localities and years (Ostman et al 2001, Schmidt et al 2003).

Although it is likely that biodiversity enhance pest control in crops, sometimes empirical evidence fails to demonstrate that increasing richness or abundance of natural enemies always translates in increased crop yield (Chaplin-Kramer *et al.* 2011). Possible explanations for this failure include the biotic mechanisms previously referred (eg. omnivory, intraguild predation and apparent competition) but also limitations in methodological approaches, which are biased to assessment of biodiversity through changes in species richness or abundance, while other characteristics of biodiversity, such as the variation in the number and type of interactions among species have been largely omitted. Given that a network approach may help in understanding the overlap of species, as well as their function in agroecosystems (Bohan *et al.* 2013) their study could provide valuable information about the role of biodiversity in pest control and other ecosystem services.

1.5 Indicators of biodiversity

Most studies assessing the role of biodiversity on pest control have used the species richness and the abundance of individuals among species as indicators of diversity (Chaplin-Kramer *et al.* 2011, Letourneau *et al.* 2011). However, there is a growing interest on evaluating changes in diversity at different spatial scales, e.g. by partitioning of biodiversity (Tscharntke *et al.* 2012), as well as by considering changes in the structure of interactions networks in agroecosytems (Bohan *et al.* 2013).

Given that ecological processes that affect diversity in agricultural landscape operate at higher spatial scales than crop fields (Tscharntke *et al.* 2012), several spatial scales should be considered in evaluating patterns in diversity in agricultural landscapes. A partitioning of diversity serves as a methodological approach to accomplish this task. This method brakes down the regional gamma diversity (γ) into independent components of local alpha diversity (α) and beta diversity (β), in a multiplicative way: $D\alpha \times D\beta = D\gamma$ (Jost 2006a). Alpha diversity is the diversity of a point location or a single sample; Beta diversity is the diversity due to multiple localities -or turnover in species composition among sites- and Gamma diversity is the diversity of a region, or at least the diversity of all species in a set of samples (Stevens 2009).

Empirical studies suggest that Beta diversity accounts for the major part of species richness in agroecosystems (Roschewitz *et al.* 2005, Clough *et al.* 2007). This increase in beta has been attributed to different factors: landscape heterogeneity, differences in habitat characteristics, low dispersal rates of organisms and deficient sampling effort. However, at larger spatial scales, landscape simplification in croplands may decrease beta diversity by increasing the probability of local extinction of rare species, as well by prompting the dominance of communities by few species, which are superior competitors in highly disturbed habitats –a process known as the 'homogenization' of ecological communities– (Arroyo-Rodríguez *et al.* 2013b).

On the other hand, crops can be viewed as islands in archipelagos or as patches in fragmented landscapes and thus they can be studied under the same perspective. An advantage of this approach is that it allows the description of species co-occurrence patterns under the theoretical framework of the metacommunity, defined as a set of local communities that are linked by dispersal of multiple potentially interacting species (Leibold *et al.* 2004). Thus, the organization of species interactions across agricultural landscapes can be described by incidence matrices summarizing which sites (columns) are occupied by which species (rows) (Leibold and Mikkelson 2002).

By studying these matrices, ecologist have found broad and repeatable patterns, which generally do not occur by chance, including nestedness, turnover and compartmentalization (Leibold and Mikkelson 2002). Nestedness indicates that species assemblages present in species-poor sites are a proper subset of those present in species-rich sites (Patterson and Atmar 1986). Compartmentalization reflects the tendency for species to replace each other from site to site (Leibold and Mikkelson 2002). However, as many networks can lead to similar patterns, a correspondence between patterns and theory does not necessarily identify the correct causal processes of these patterns (Werner 1998), but may give insights into the hypothesis about their mechanistic explanation (Price et al 2012).

Mechanisms for nestedness include passive sampling, neutrality, differential colonization or extinction among species along environmental or biological gradients (area, isolation, quality) of the target patches (Ulrich *et al.* 2009). Meanwhile, for compartmentalization major habitat divisions (Pimm and Lawton 1980) and habitat specialization have been proposed as the major drivers. Identifying these patterns provides insights into recognizing which species are more sensitive to habitat fragmentation, as well as understanding how species respond to environmental gradients; this information is useful in designing strategies for conserving biodiversity, e.g. a single large area if metacommunities are nested or several smaller areas if they are compartmentalized (Mendez 2004).

Interaction Networks. Ecological networks provide a complete and easy to understand description of biodiversity, interactions between species and the structure and function of ecosystems (Dunne *et al.* 2002, Memmott 2009). Species interaction networks are useful to provide comparable descriptions of the organization of local communities (Bascompte and Jordano 2007). Network analysis help into identifying keystones species or functional groups that contribute to the ecological function as well as to the stability and resilience of agroecosystems (Bohan *et al.* 2013).

Typically network ecology has focused on three types of interactions: trophic (resource - consumer), mutualistic (pollination and frugivory) or host-parasitoid (Ings *et al.* 2009). These interactions can be described by bipartite networks, which are built from matrices in which rows represent one set of species (e. g., plants) and columns represent another set of species (e.g., herbivores).

Several metrics have been developed to describe the structure of these networks (Bluethgen *et al.* 2008). Most basic metrics include: network size –or the total number of species or “nodes” involved in interactions-, the connectance –a measure of the density of links in the web-, the degree of each node –or the number of links per species, and the degree distribution. In addition, interactions networks may have nested structures as well as modular structures (Lewinsohn *et al.* 2006). Nestedness arises when species with fewer interactions are preferentially associated with a subset of species that interact with the most connected ones (Bascompte *et al.* 2003), whilst modularity arises when a group of species interact more often with species within the group than with the rest of the species in the network (Krause *et al.* 2003, Lewinsohn *et al.* 2006, Guimerà *et al.* 2010).

These patterns have been proposed as a mechanism for stability of species assemblages. For instance, a nested interaction structure might buffer communities against extinctions or temporal fluctuations in the abundance of specialist species (Canard *et al.* 2012), and may reduce competition and then promote species coexistence and biodiversity (Bastolla *et al.*

2009). Modularity could increase the stability of interaction networks since the compartments retain the impact of a disturbance within a single compartment, minimizing impacts on other compartments in the food web (Krause *et al.* 2003), although strong compartmentalization may result in fragmentation of communities (Guimerà *et al.* 2010, Thebault and Fontaine 2010).

In agroecosystems, a network interaction approach has been used to explore the effects of land-use intensification on species interactions, as well as, in their associated ecological functions. Comparisons of networks structure between organic and conventional farming confirmed more diverse assemblages of plants and arthropods, as along with, more stables rates of parasitism under organic management (Macfadyen *et al.* 2009, Macfadyen *et al.* 2011a). Some studies evaluating the influence of landscape structure on interactions networks in agroecosystems indicate that land-use intensification induces strong changes in network structure. For instance, in intensively managed agricultural habitats most energy flows along one or few pathways (Tylianakis *et al.* 2007), and modularity may increase (Macfadyen *et al.* 2011b). Although landscape simplification is generally associated to loss of biodiversity, not always a complex landscape is associated with a more complex network structure. For instance, a lower complexity was reported for aphid-parasitoid interactions in complex landscapes (Gagic *et al.* 2011), due to higher dominance of one species of aphid in such landscape.

Network analysis is being used to evaluate how the robustness of interaction networks -a measure of network's vulnerability to species loss- varies across gradients of land use intensification and among different types of networks present in agroecosystems. From these studies it is known that aphid, insect seed feeder, and pollinator networks appeared more fragile to local extinction of species (Pocock *et al.* 2012), whereas in host-parasitoids networks empirical evidence does not support the idea that land-use intensification influences negatively the robustness of ecological networks (Macfadyen *et al.* 2011b). However, these conclusions have been drawn from few studies, thus more research in this field is needed to establish clear patterns in networks' robustness in agricultural environments.

Finally, the length of food chains is an important structural property required for top-down control of agricultural pests. The efficiency of biological control might depend on the number of trophic levels in the agricultural network, as well as, on the diversity within each one (Bohan *et al.* 2013). Besides diversity, further network analysis should consider plant quality, given that their characteristics can have strong bottom-up effects on herbivores like aphids an their natural enemies (Bohan et al 2007, Bukovinsky et al 2008, Lohaus et al 2013). Furthermore, network analysis may help in identifying the plant taxa that can potentially lead to disproportionate gains in biodiversity (Pocock *et al.* 2012).

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2. Study Area

2.1 Location

Topaipí is a municipality in the Río Negro Province in Cundinamarca department, approximately 141 km northwest of Bogotá (Fig.2-1).The municipality stands at 1323 m altitude in the Western Cordillera of the Colombian Andes (5º 20´ 17´´N and 74º 18´ 21´´W).

Figure 2-1. Location of Topaipí in the context of South America and Colombia

Topaipi was founded in 1806 and declared a municipality in 1927 officially (EOT, 2004). It comprises an area of 150.04 km^2 and is bordered to the north by the Yacopí municipality, to the east by the municipalities of Pacho, Paime and Villa Gomez, to the west by La Palma municipality, to the south by the municipalities of El Peñón and Pacho.

2.2 Climate

No site specific climatic data are available for the study area, and therefore the statistics for three closer meteorological stations (Yacopí: 5° 29´ N ‘ 74° 21´ W; Paime: 5° 22´ N ‘ 74° 9´ W; La Palma: 5° 20´ N ‘ 74° 23´W) were used to describe the climate of the area. Topaipí has a subtropical climate influenced by the northeastern trade winds. Rainfall is bimodal with an average annual of 2521 mm which peaks in April and October (Figure 2-2.). The average temperature is 21.3 °C and it varies between 19.9 °C and 23.5 °C.

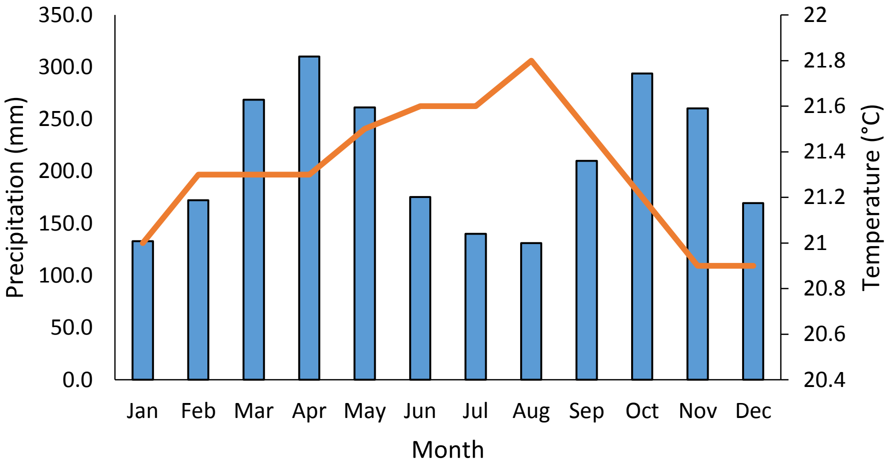

Figure 2-2. Multiyear average monthly rainfall and temperature (1992-2011) based on climatological data from three stations: La Palma, Paime and Yacopi.

2.3 Environmental issues

Topography is dominated by mountainous slopes, in which mass movements are a common phenomenon. Soils are acidic (average pH 4.8) with sandy loam to clay loam. Life zone is Premontane wet forest (Holdridge 1967) whose natural vegetation is an evergreen forest (30- 40 m tall) with abundant epiphytism.

Hydric resources are abundant and are distributed among approximately 160 streams. Main rivers include *Río Murca*, *Río Minero* and *Río Bunque* which are tributaries of the Río Negro (EOT 2004). Most water is used for human consumption, which are delivered to population through a sewer system or through hoses. Although agriculture is performed without irrigation, water is taken up for local small hatcheries of Tilapia (*Oreochromis* spp.)

The landscape in this region is a mosaic of native forest and human land-uses such as cultivated fields, fallows and pastures; but still forest covers more than 50% of the municipality (EMP Unpublished data). Extensive grazing of cattle is the main source of farmers' livelihood, but they also grow marketable crops such as coffee and sugar cane.

Subsistence crops included cassava, plantains and corn, which are mainly grown on steep slopes close to remnants of native forest. However, some farmers also grow these crops in more transformed areas such as home gardens.

2.4 Socio economic issues

Population. Topaipi population decreased by 22% between 1993 and 2005. The 1993 Colombia Census reported a population of 6182, while the 2005 Census reported a population of 4187. The intensity of violence suffered in this period led to large population movements as people left rural communities in fear of their lives. These movements were forced by the war between guerrillas and paramilitaries

According to data reported by Arenas (2008), most population inhabits rural areas (85%) with 1467 people (39.7%) under the age of 20, 1489 people (40.3%) aged 20-60, and 711 (20.0%) who were 61 years of age or older. For every 100 males there were 83 females (Figure 2-3).

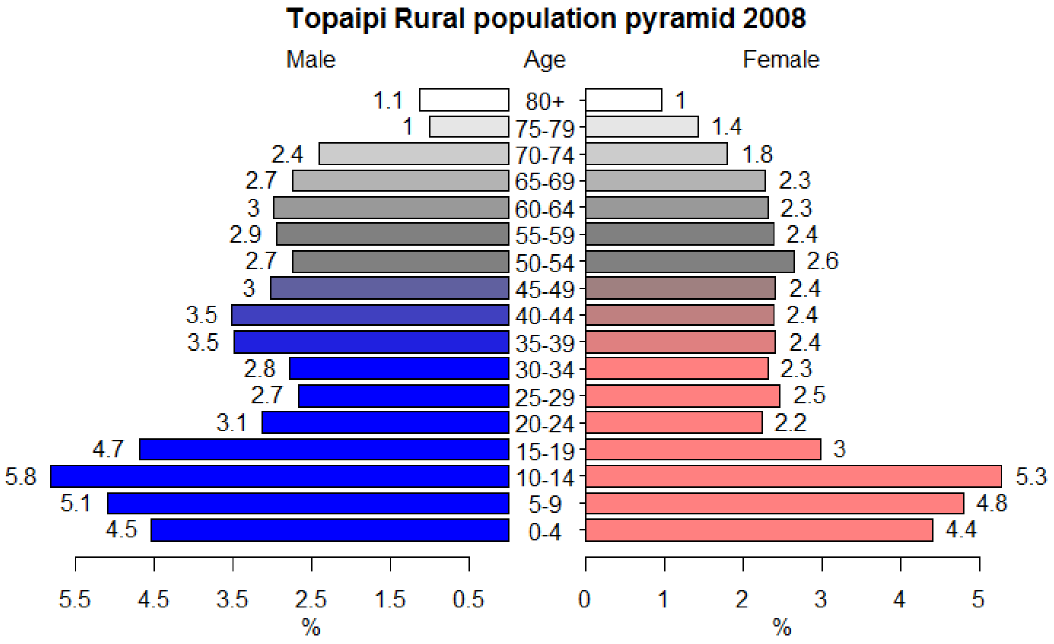

Figure 2-3. Topaipi rural population pyramid 2008, based on data reported by Arenas (2008).

Sixty three percent of population had Unsatisfied Basic Needs (UBN), and 32.9% of population suffered from extreme poverty caused by inequality (Arenas, 2008). Poverty is more critical in the rural area, where UBN was 69.61% compared to 29.49% in the urban area. According to Sisben data (2007), 83% of population was classified in category one, followed by a 16.7% in category two.

Land Tenure and Farming System. Topaipi is characterized as being economically dependent on the agricultural sector, mostly on coffee and sugar cane. The municipality had a smallholder distribution of property. 2828 landowners (64.4%) had farms averaging 5 hectares or less, which accounts for 64% (1729 farms) of the total number of farms in the municipality (Figure 2-4).

Agricultural production is characterized by having limited access to resources such as land and capital. Food production is mainly based on family labor and; most of the household income is derived from agricultural activities. For some crops like corn, production is for own consumption, whereas other crops such as coffee or sugar cane, production is sold in local markets. These conditions indicate that family farming is the dominant production system in Topaipi. Some productive units correspond to subsistence agriculture, while the other ones are in the transition to a consolidated family farming, in the sense described by FAO- IDB (2007).

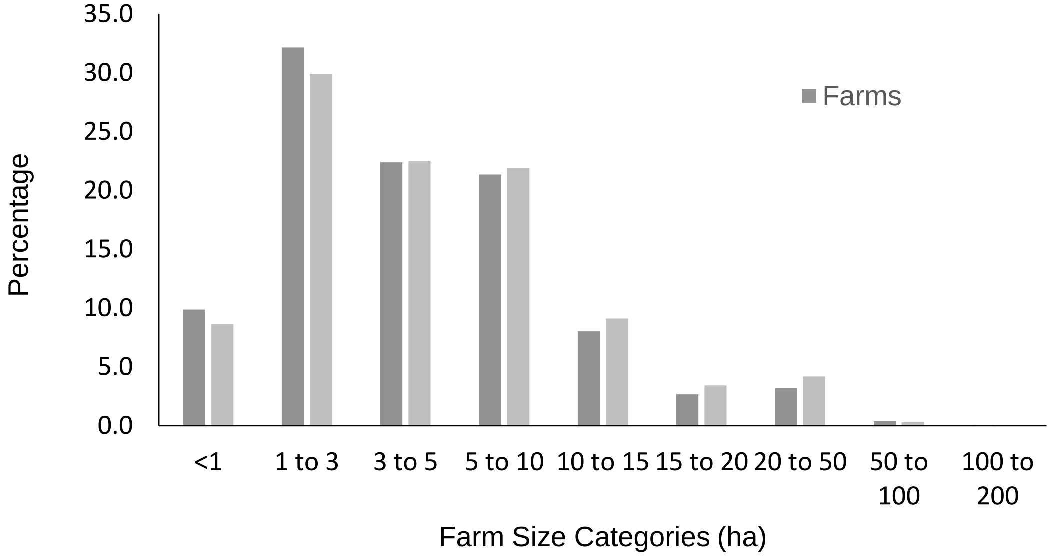

Figure 2-4. Percentage of farms units and landholders according to farm size categories. The graph was constructed based on data reported by Arenas (2008).

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3. Habitat heterogeneity induces plant and arthropod species turnover in traditional cornfields

Abstract

The expansion of the agricultural frontier by clearing remnant forests has led to landscape simplification in low-Andean tropical regions. Landscape simplification reduces the richness and abundance of arthropods in crop systems. Previous studies have evaluated the effect of natural habitats on arthropod diversity at local spatial scales in temperate regions, and little is known about their effects in more complex crop systems, such as tropical traditional crop systems that maintain a high diversity of weeds in addition to arthropods. To understand the factors that influence patterns of diversity in human-dominated landscapes, we investigated the effect of remnant forest on plant and arthropod diversity in traditionally managed corn crops.

We conducted surveys of plants and arthropods in twelve traditional cornfields in the Colombian Andes during the second growing season in 2011. We estimated alpha and beta diversity to analyze changes in diversity related to forest cover within a radius of 250 m around each cornfield.

We determined that the alpha diversity of plants and arthropods in cornfields was not associated with higher forest cover surrounding each field. Instead, the former land use of each cornfield affected local plant diversity, and plant diversity was positively related to the alpha diversity of herbivores. However, we determined that forest cover influenced changes in plant species composition and the turnover of herbivore communities among the cornfields. Dominant plant species varied among fields, resulting in high differentiation of plant communities. Predator communities also exhibited high turnover among cornfields, but differences in composition arose mainly among rare species.

The crop system evaluated is a highly heterogeneous habitat due to its landscape configuration, high diversity of weeds and variations in historic land use among the cornfields. Thus, these factors should be considered for diversity conservation and the development of sustainable pest management strategies in simplified agroecosystems.

Keywords: Agrobiodiversity, Andean crops, Beta diversity, Habitat heterogeneity, Landscape complexity, Weed richness, Arthropod richness, True diversities, Zea mays L.

Introduction

Agroecologists propose that traditional farming systems may provide scientists with invaluable agro-ecological principles needed to develop global sustainable agriculture (Altieri 1991). These principles are useful in developing strategies for pest management in crops as well as conservation of biodiversity in human-modified landscapes. Indeed, traditional agriculture sustains a huge diversity of organisms that in some cases may be comparable to that of natural ecosystems (Settle *et al.* 1996). This diversity benefits agroecosystems through its positive effect on ecosystem functioning, increasing adaptability to extreme climatic conditions and resilience to biotic and abiotic stress (Kahane *et al.* 2013). However, underestimation of traditional knowledge, intensification of small family farming (Oyarzun *et al.* 2013), and rural-urban migration (Grau and Aide 2008) have led to the abandonment of traditional agriculture. The combination of these factors results in an irreparable loss of native varieties of crops, their wild relatives, and associated biota that perform essential ecological functions for agriculture (e.g., pest regulation, pollination and nitrogen fixation, etc.). Therefore, for agroecologists must elucidate how traditional farming systems prevent the loss of biodiversity, a key factor for achieving sustainable agriculture.

Assessments of biodiversity in human-dominated landscapes indicates that less-intensive land use has a positive effect on biodiversity (Tylianakis *et al.* 2006, Tscharntke *et al.* 2012). For example, comparison of biodiversity between organic and conventional farms has demonstrated that the species richness of weeds and beneficial arthropods is higher in organic fields (Clough *et al.* 2006, Holzschuh *et al.* 2006, Holzschuh *et al.* 2008, Pluess *et al.* 2010, Letourneau *et al.* 2012a). At the landscape level, the presence of natural habitats may favor the species richness and abundance of beneficial arthropods in crops (Schmidt *et al.* 2005, Schmidt *et al.* 2008, Gardiner *et al.* 2009, Letourneau *et al.* 2012a). Although these findings are consistent across different regions and crops (Chaplin-Kramer *et al.* 2011), the methodological approaches of these studies have been criticized because they have mainly focused on the diversity at the plot-scale (Tylianakis *et al.* 2006, Clough *et al.* 2007). Analysis of local diversity alone cannot capture all the processes that determine species richness at higher spatial scales (Tylianakis *et al.* 2006, Clough *et al.* 2007, Tscharntke *et al.* 2012). Consequently, the impacts of human activities on biodiversity in agricultural landscapes should consider different spatial scales, in order to gain more insight into the relationships among landscape structure, crop management practices and biodiversity.

To tackle this challenge, a growing number of studies have partitioned of diversity into components (alpha, beta and gamma diversity) to assess the effects of crop management practices and landscape structure on biodiversity in agroecosystems (Roschewitz *et al.* 2005, Tylianakis *et al.* 2006, Clough *et al.* 2007, Poggio *et al.* 2010, Armengot *et al.* 2012). Based on these studies, agroecologists have suggested that intensifying agriculture (through the transformation of natural habitats to agriculture or through crop management practices to increase crop yields) may homogenize biological communities across agricultural landscapes (Tylianakis *et al.* 2006, Armengot *et al.* 2012). Accordingly, we would expect the contribution of local diversity to overall diversity (gamma) to increase as the agroecosystem management becomes more intense, which is referred to as low beta diversity (Tylianakis *et al.* 2006). This homogenization may arise either from the reduced availability of niches in simplified habitats, which can promote the loss of rare or habitat specialist species, or from the dominance of disturbance-adapted species that can dominate biological communities (Arroyo-Rodríguez *et al.* 2013a).

However, agricultural intensification may also differentiate communities across agricultural landscapes; in this case, we would expect beta diversity to increase as land use intensifies. For instance, a higher contribution of beta diversity to overall diversity has been observed for weeds (Roschewitz *et al.* 2005) and arthropods (Clough *et al.* 2007) in temperate agroecosystems. Such differentiation may occur if the landscape configuration restricts the dispersion of organisms across different habitats. For example, food production activities result in habitat patchiness in the landscape, which in turn promotes differentiation of communities through extinction-colonization dynamics (Jimenez-Valverde *et al.* 2010). These processes are highly dependent on the spatial scale and the organisms' life history traits, although geographical distances between plots and similarities in the environmental conditions might also be important predictors of changes in the composition of species (Jimenez-Valverde *et al.* 2010).

In this article, we aim to study the biodiversity of plants and arthropods in traditional cornfields located in a mountainous environment in the Colombian Andes. Biodiversity inventories were conducted in cornfields because corn is a native crop whose management practices remain in a traditional way (in contrast to introduced crops such as coffee or sugar cane). We analyzed diversity data with a multi-taxonomic focus (plants, herbivores and predators) and multi-scale perspective (within fields and among fields). In this context, we addressed the following questions. *i)* How does alpha diversity change across a gradient of forest cover for different taxa in this area? *ii)* To what extent does beta diversity changes among different taxa and among rare and common species? *iii)* Are there environmental factors related to differences in species composition among cornfields? and, *iv)* How do species composition and the relative abundance of species vary among cornfields?

Because a higher amount of natural habitats in agroecosystems is associated with higher species richness of arthropods in crops (Chaplin-Kramer *et al.* 2011), we expected that the biodiversity of plants and arthropods in cornfields would increase with increasing forest cover surrounding the crop. Due to the long human land-use history in this region (farmers have found archaeological remains of indigenous cultures) and distribution of the cornfields within a small area, we also predicted a low diversity in general for these plots. More importantly, the same species should be everywhere. Hence, we expected few changes in species composition and similar patterns of relative abundance, such that a few species should dominate all fields. Consequently, we hypothesized that beta diversity is low among cornfields, because most species should be everywhere and the dominant species should not vary. We also expected the geographical distance between cornfields to explain the replacement of species with higher beta diversity as the distance between cornfields increased.

Materials and Methods

Study area. Fieldwork was conducted from August 2011 to February 2012 in the municipality of Topaipí, Cundinamarca; a rural area located on the west slope of the Central

Cordillera in Colombian Andes (5 23.366N, 74 18.125W). In this region, we choose twelve traditional cornfields with a minimum distance of 230 m from each other. All fields had small areas, which varied from 591 to 5112 m^2. Cornfields were embedded in a landscape sector of 14 km^2 in an altitudinal gradient ranging from 1296 to 1550 m.

The landscape in this region is a mosaic of native forest and human land use such as cultivated fields, fallows and pastures, and but forest still covers more than 30% of the municipality (Riveros 2013). Annual rainfall in the region is 2525.8 mm, with peaks in April and September, and the average temperature is 21.3°C with a range of 19.9 to 23.3 °C. Extensive grazing is the main source of livelihood for farmers, who also grow marketable crops such as coffee and sugar cane. Subsistence crops included cassava and corn, which are mainly grown on steep slopes close to remnants of native forest. However, some farmers also grow these crops in more transformed areas such as home gardens.

Crop management. Although corn is a semiannual crop, farmers prefer to sow it only in the second season of the year in order to avoid pest problems. Therefore, land is prepared for sowing in mid-July to mid-August, primarily by slash-and-burn agriculture. Farmers sown after mid-August and the emergence of corn seedlings corresponds with the onset of rains in the beginning of September. Farmers also perform hand weeding between 7-8 weeks after corn emergence, and they do not use chemical control of insect pests. Although peasants partially harvest of corncobs in November, they allow the crop to dry until February or March, when the cornfield is harvested. Most of the crop biomass remains in the weedy field until the next crop season. In most cases, this cycle is repeated for 3 or 4 years, followed by a fallow period of variable length.

Forest cover surrounding cornfields and other environmental descriptors. We registered the geographical coordinates, the altitude and the area for each cornfield by using a GPS. We mapped the land-use types within a radius of 250 m around each cornfield, via field visits and inspections of aerial photographs (GSD = 27.7 cm), and then we estimated the amount of area covered by each-land use type using Acview 3.2 (ESRI 1999). We classified land-use types in the study area as native forest, secondary growth, hedges, pastures, transitional crops, perennial crops, home gardens and constructions.

The forest cover surrounding each crop was selected as the main predictor for further analysis. We observed a gradient in the proportion of forest from 0 to 62% among the twelve cornfields selected. This variable was negatively related to cropped area (Pearson's r = -0.80, p = 0.0017) and to habitat heterogeneity (r = -0.87, p = 0.0007), which was measured as the Shannon's Index for landscape data (Turner 1989).

To evaluate possible co-varying effects of soil quality on measurements of diversity, we sampled the soil in each plot at harvest time. Because the introduction of organic matter into soils may increase biomass and species numbers (Pimentel and Krummel 1987, Paoletti *et al.* 1992), we chose the percentage of carbon in soils as a predictor of species richness for further analysis. We also included as co-variables altitude, the perimeter-to-area ratio of each field, and the previous land use of the cornfield.

The previous use of the plots differed among the cornfields. Therefore, we registered at the beginning of the study, we registered the former type of cover of each field. Five categories were established: native forest, fallows (secondary growth), pastures, other crops and invaded plots, which differed from fallow plots because these fields were dominated by a unique plant species.

Arthropod Sampling. We sampled flying and leaf-dwelling arthropods on September and December 2011. Samples were obtained by sweep netting (N= 10 strikes) at the center of each cornfield. Arthropods were preserved in 70% alcohol until further identification of family level and morpho-species of herbivores and predators. We classified arthropods into five trophic groups (predators, parasitoids, herbivores, pollinators, nectarivores and saprophagous), according to reports in the literature for families or genera (Kaston 1978b, Wharton *et al.* 1997, Triplehorn and Johnson 2005, Fernández and Sharkey 2006b, Dippenaar-Schoeman and Jocqué 2007b).

Weed Sampling. We sampled plants on December 2011, four months after the corn sowing date. We randomly selected five rows in the center of each cornfield. For each row, we used equidistant sampling stations along a 20-meter-long transect, thus totaling 25 sampling stations per cornfield. Each station was sampled by using a plastic quadrat (50 cm x 50 cm) divided in 100 subquadrats. We recorded the presence of all plant species in each station and counted the number of subquadrats occupied by each species as a measure of cover.

A measure of dominance of each species per cornfield was estimated as the sum of their relative values of frequency and coverage. The relative frequency was estimated as the proportion of quadrats in which the species was present in each cornfield, whereas the relative coverage was the sum of the coverage of each species in all quadrants divided by the sum of the values of coverage for all species in each cornfield.

Data analysis. Sample completeness in each cornfield was evaluated as the percentage of species observed relative to the number of species predicted by the Abundance Coverage-based Estimator of species richness (ACE) by using EstimateS ver. 8.2 (Colwell 2009). In addition, we estimated the sampling coverage of our data: these values represent the proportion of the total number of individuals in a community that belong to the species represented in a sample (Chao and Jost 2012).

Local diversity. We calculated the Hill numbers, or “true diversities” of each cornfield by following the methodological approach developed by Jost (2006). According to that method, common diversity indexes are converted into measures of diversity in the community, which are known as the “effective number of species” and obey the duplication principle (Jost 2006b). We calculated these numbers at three different orders (q) of diversity. The order q indicates the measurement’s sensitivity to common and rare species. A q value of 0 is indifferent to species abundance, such that all species are given the same weight, thereby favoring rare species. When q = 1, species are weighted exactly for their abundance in the community, rare or common species are not favored, whereas q = 2 favors the more abundant species (Jost 2006b). According to the above, species richness is a measure of diversity of order zero (${}^{0}D$), the exponential Shannon’s index is the measure of diversity of order one (${}^{1}D$), and the inverse of Simpson’s index is a measure of order two (${}^{2}D$) (Jost 2006b, 2007). We constructed diversity profiles by plotting diversities at different orders in an increasing manner, which allowed us to identify patterns of dominance in cornfield communities. True diversities were calculated using R and a modified version of the Entropy calculator, an excel code developed by L. Jost.

We used linear regression models to analyze possible relationships among diversity and cornfield characteristics. We used true diversities of plants, herbivores and predators as the response variables, whereas the proportion of forest cover within a radius of 250 m around each cornfield was tested as the main predictor. To identify possible co-varying effects of the other characteristics of the cornfields, we included altitude, field perimeter-to-area ratio, soil organic matter content per field and the former land-use of each field in the models. We used a forward stepwise selection procedure to simplify the models. These analyses were performed in R (R Development Core Team, 2008).

Turnover of species between cornfields. We used multiplicative diversity partitioning of Hill numbers, in their unweighted form, to analyze the changes in species composition between cornfields (Jost 2006b). This method partitions the regional gamma diversity (γ) into independent components of local alpha diversity (α) and beta diversity (β), in a multiplicative manner: Dα × Dβ = Dγ (Jost 2006b). Beta diversity can be transformed into values between 0 (all sampling units have different species) and 1 (all sampling units have the same species) as follows:

$${}^{q}CS = (1/{}^{q}D_{\beta} - 1/N)/(1 - 1/N) \qquad \textbf{Eq. 1 Compositional similarity}$$

When q = 0 and N = 2, the result is the Jaccard Index; when q = 2 the result is the Morisita-Horn-Index. This transformation is useful when comparing values based on a different number of sampling units (Jost 2007).

We performed a Mantel test to evaluate whether the variation in the pairwise beta diversity of cornfields was related to pairwise crop distance. In addition, we performed a Mantel test between the pairwise beta diversity matrices and the environmental distance matrices to determine if the dissimilarity in species composition was related to environmental gradients. Environmental distance matrices were constructed based on pairwise differences between cornfields, including forest cover surrounding each cornfield, altitude, percentage of soil organic matter and the number of plant species in each cornfield. Correlation coefficients and p-values were estimated from 1000 permutations. Pairwise beta diversity matrices and the Mantel Test were performed in R (R Development Core Team, 2008).

Patterns of relative abundance. For each cornfield we ranked species according to their abundance from the highest to the lowest values. We plotted the abundance of the ten most dominant species in each corn field. These graphs allowed us to identify changes in the dominance and in the composition of the more abundant species among the cornfields.

Context-dependent changes in species composition. We performed Non-Multidimensional Scaling analysis to visualize changes in species compositions as a function of the landscape context of the cornfields. Ordination was undertaken for quantitative data using the Jaccard index and Morisita-Horn index, which are also direct transformations of beta diversity of order 0 and 2, respectively. The stress values of each analysis are reported in the results. These analyses were performed in R (R Development Core Team, 2008).

Results

We collected 198 morpho-species of plants from 29 orders and 53 families; 5975 individuals of herbivores from 5 orders, 38 families and 217 morpho-species; and 1574 individuals of predators from 7 orders, 34 families and 132 morpho-species. According to the ACE richness estimator, we sampled 83% and 70% of the total estimated number of plant and arthropod species, respectively, in the community. However, when we used sampling coverage values, we obtained coverage values of 90% to 95% which indicates that just 5% to 10% of individuals belonged to species not represented in our sampling. Therefore, we conclude that our sampling was sufficient to characterize the plant and arthropod communities within the cornfields.

Local diversity. Alpha diversity profiles (Fig. 3-1) revealed that most of the species richness in each cornfield was attributable to rare species. In addition, we observed a large decrease in the effective number of species or true diversities as the order of diversity (q) increased, indicating a high degree of dominance in the community. This pattern of dominance was consistent throughout all cornfields and all taxonomic groups. Furthermore, high dominance of communities of plants and arthropods within the cornfields occurred regardless of whether the field was mainly surrounded by agricultural covers (A1-A6 cornfields) or by native forest (F1-F6 cornfields).

Our data also indicated a significant relationship between the proportion of native forest surrounding each cornfield and the local diversity of plants, as well with predators (q=1) and (See Appendix 2-1). However, we determined that other factors, such as the former land-use of the cornfield and the diversity of plants was consistently related to the diversity of organisms in the studied fields. The former land use of the crop field affected the diversity of plants regardless of the order of diversity considered (see Appendix 2-1, Fig. 2-2). In particular, the lowest values of plant diversity were observed in fields which, prior to being sown with corn, were invaded by a dominant plant (e.g., *Hedychium coronarium* Koening or *Gynerium sagitatum* Aubl.). Similarly, dominant and typical species of predators also had the lowest values of diversity in these invaded plots (Fig.3-2, see Appendix 3-2).

We observed a strong positive relationship between herbivore diversity of this group and the diversity of typical plant species (q=1). This pattern was similar for all three orders of herbivore diversity (Fig. 3-3, Appendix 3-2).

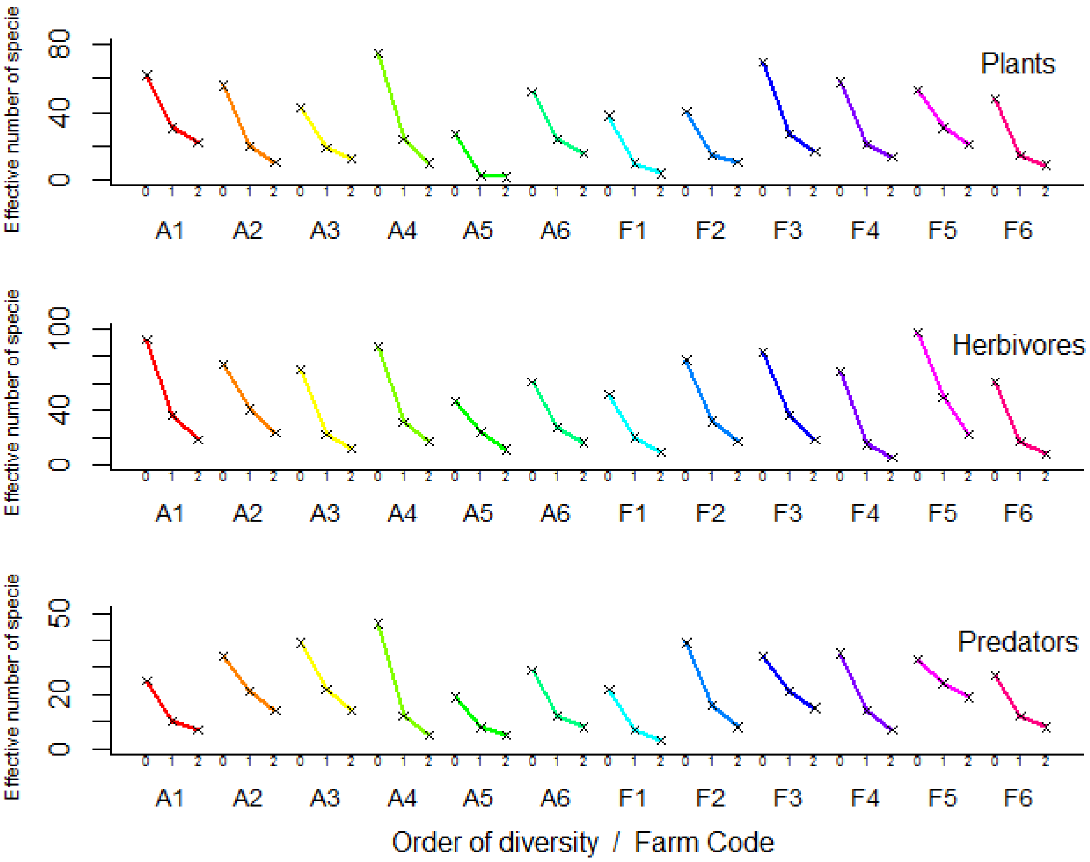


Figure 3-1. *Alpha diversity profiles of plants, herbivores and predators in 12 traditional cornfields at a locality in Topaipí (Colombian Andes). The cornfields are arranged in ascending way, according to the proportion of forest within a radius of 250 m cornfield. A1-A6 were cornfields mainly surrounded by agricultural covers, whereas F1-F6 cornfields were mainly surrounded by native forest.*

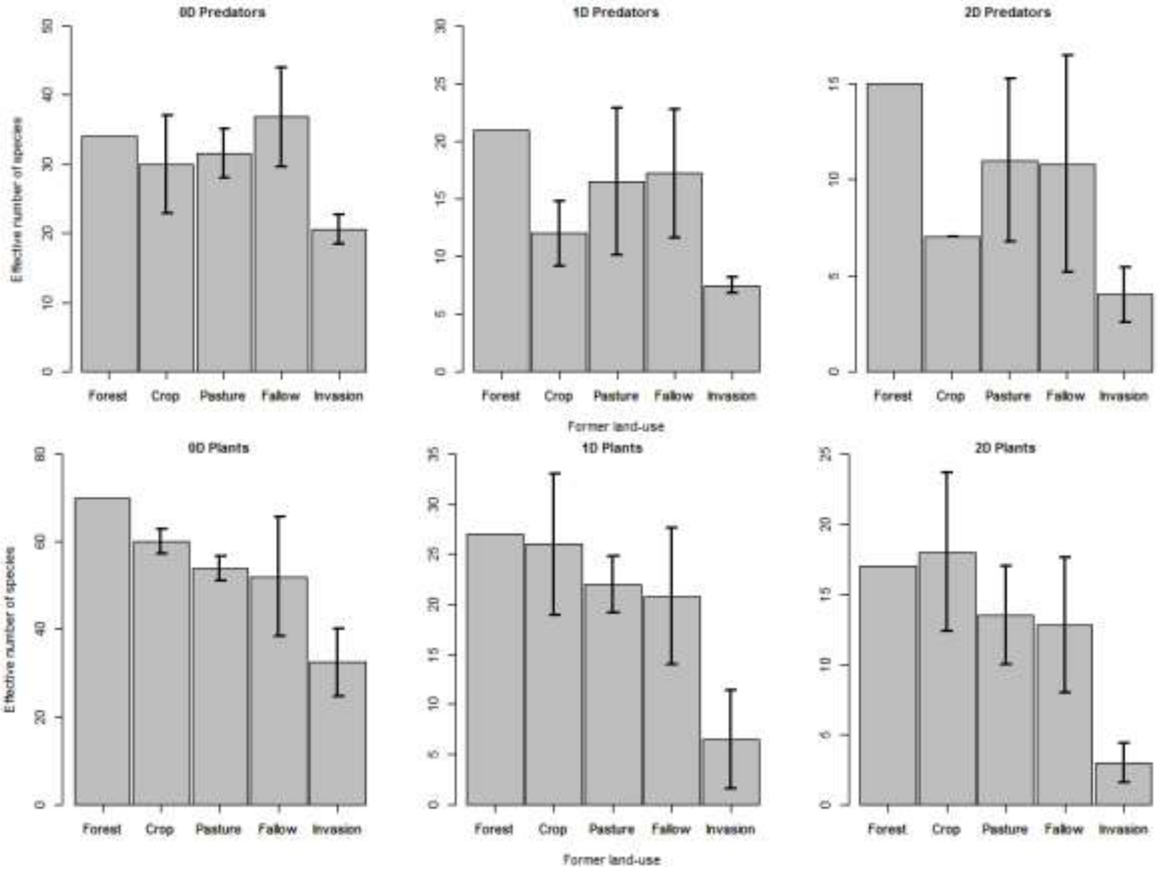


Figure 3-2. Effective number of plant and predator species according to the previous land-use of the cornfields. Bars represent Mean ± 1 SD. The order of diversity is included as a prefix: 0D for all species, 1D for typical species and 2D for common species. Former land-use includes forest (n=1), crops (n=2), pasture (n=2), fallow (n=5) and invasion (n=2).

Finally, regression analysis revealed a significant but inconsistent relationship between the diversity of the dominant species (q=2) of all taxa and the perimeter-to-area ratio of cornfields. Similarly, the diversity of herbivores was significantly related to altitude but the predictive value of the independent variable was limited (see Appendix 3-2).

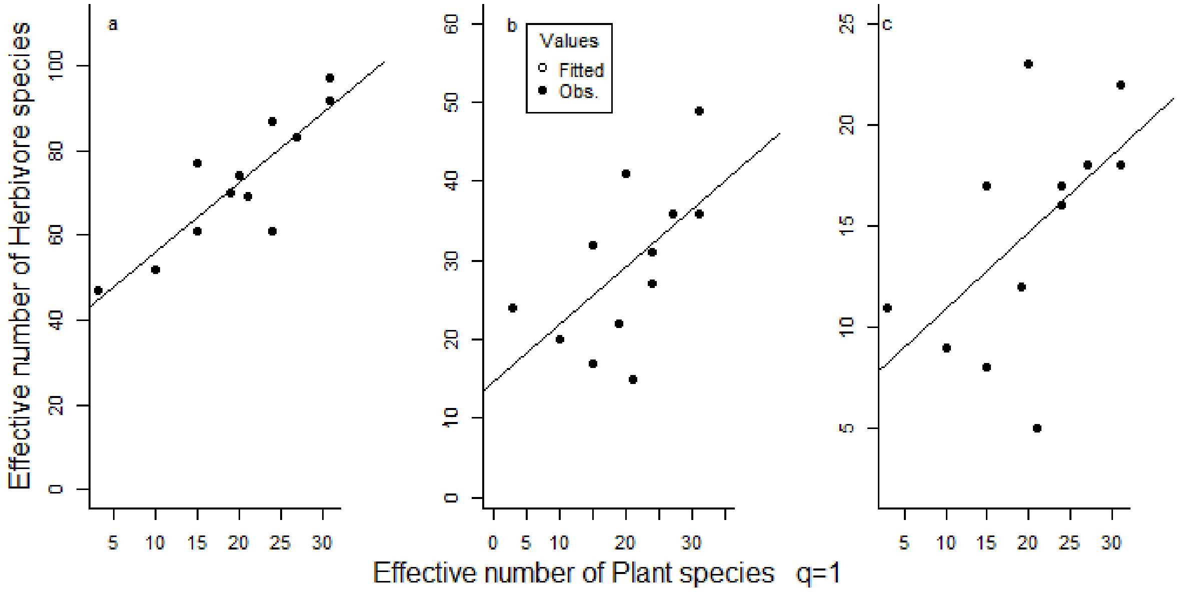


Figure 3-3. Relationships between the diversity of herbivores and plants in cornfields: a) *for all species q = 0,* b) *for typical species or q = 1 and, c) for common species or q =2. Fitted values (lines) were calculated from Poisson regression models using the effective number of plants at q=1, as a predictor for the effective number of herbivores.*

Species turnover among cornfields. Beta diversity profiles indicated that the turnover of species among cornfields differed for plants and arthropods. Plant beta diversity increased as the order of diversity increased, whereas arthropod beta diversity decreased (Fig. 3-4). Consequently, the highest differences in species composition among cornfields were stronger among abundant plant species, whereas for arthropods these differences arose among rare species, particularly for predators.

Because we evaluated 12 cornfields in our study area, the true beta diversities could range in value from 1 to 12, providing an estimate of the number of effective communities in this landscape. These values for our data ranged from 1.8 to 5.2, with the lowest values for herbivores and the highest values for plant communities, regardless of the order of diversity considered (Table 3-1). Therefore, plant communities in this landscape tended to be different among cornfields, particularly dominant species, whereas herbivore communities tended to be more homogeneous (Table 3-1). Common and abundant species of predators tended to be the same for most of the cornfields, whereas, rare species were substantially different among them.

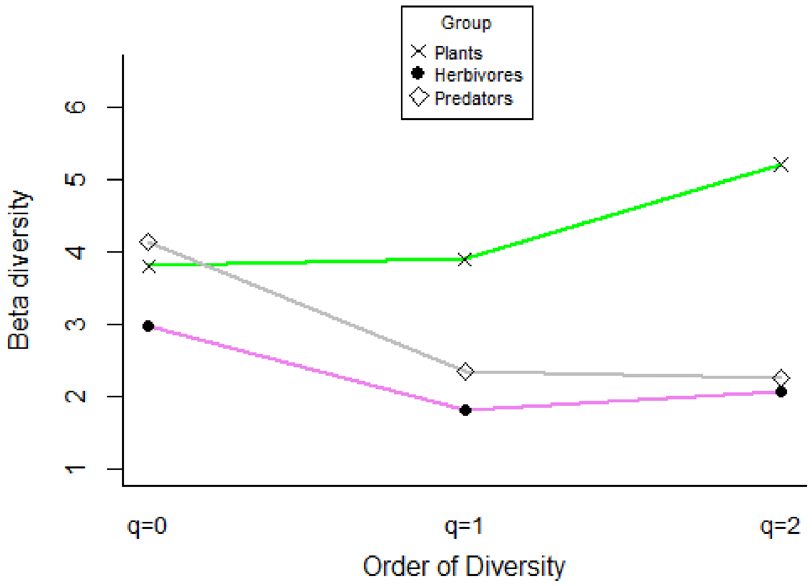


Figure 3-4. Beta diversity profiles of plants, arthropods and predators collected in twelve traditional cornfields immersed in an area of 14 km^2 in the Colombian Andes. The order of diversity indicates the measurement's sensitivity to common and rare species.

Table 3-1 True diversities of plants, herbivores and predators collected in twelve traditional cornfields in an area of 14 km^2 in the Colombian Andes.

Order of diversity	Alpha	Beta	Gamma	Homogeneity (α/γ)
Plants:				
q=0	52	3.8	198	0.26
q=1	18	3.9	70	0.26
q=2	8	5.2	42	0.19
Herbivores:				
q=0	73	2.9	217	0.33
q=1	28	1.8	51	0.55
q=2	12	2.1	25	0.48
Predators:				
q=0	32	4.1	132	0.24
q=1	14	2.4	33	0.42
q=2	7	2.3	16	0.44

Spatial autocorrelation and relationships between beta diversity and environmental gradients. We did not find evidence for spatial autocorrelation in the dissimilarity of species composition (pairwise beta diversity matrices) and the geographical distance between cornfields (Table 3-2). By contrast, we determined that the turnover of herbivores between cornfields was associated with environmental gradients in forest cover surrounding the crop and differences in plant species richness between crop fields (Table 3-2). Therefore, the greater the difference in forest cover between two cornfields, the greater the difference in their herbivore communities (q = 1). In addition, our data suggested that increasing differences in the number of plant species between cornfields are associated with higher replacement of herbivore species between cornfields.

Table 3-2. *Pearsons's r correlation from the Mantel test between Pairwise Beta Diversity matrices and distance matrices for geographical location and environmental gradients in twelve traditional cornfields. Environmental gradients included differences between fields in altitude, proportion of native forest in a radio of 250m from the centroid of each cornfield, percentage of soil organic matter (S. O. M.) and Plant species richness. Asterisk following each value indicates significant correlations at 95% of confidence.*

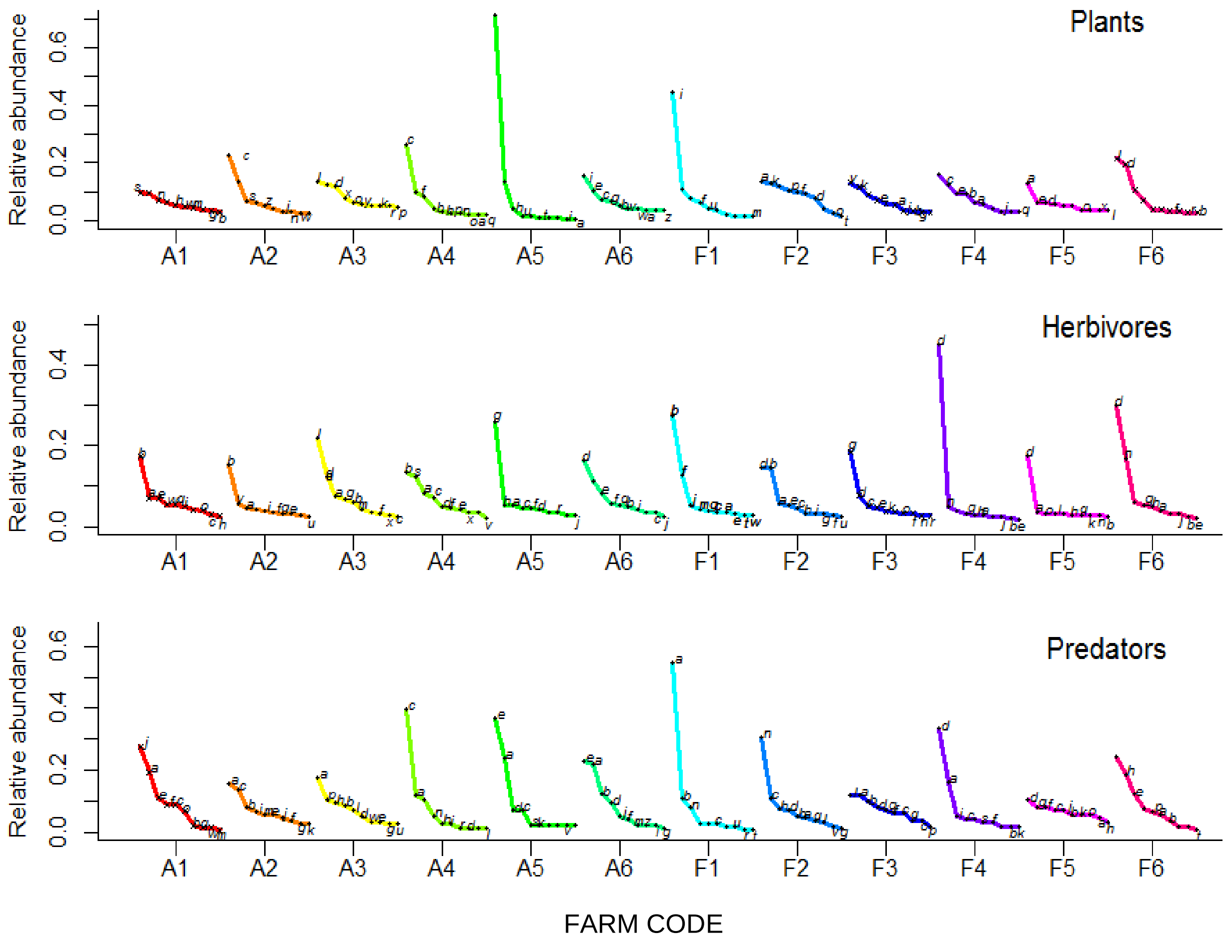
Group	Order of diversity	Geographical distance	Differences in altitude	Differences in forest cover surrounded the crop	Differences in soil organic matter	Differences in plant species richness
Plants	q = 0	-0.04	0.15	0.04	0.13	
	q = 1	-0.19	0.07	0.04	0.18	
	q = 2	-0.17	0.01	0.09	0.19	
Herbivores	q = 0	0.03	-0.06	0.06	0.02	**0.33***
	q = 1	0.08	0.05	**0.23***	0.21	0.05
	q = 2	0.07	0.13	0.21	0.12	0.01
Predators	q = 0	-0.21	0.01	-0.19	-0.02	-0.02
	q = 1	-0.16	0.02	-0.20	0.00	0.04
	q = 2	0.06	0.10	0.05	0.12	0.14

Relative abundance patterns and changes in species composition.

Rank-abundance curves for the ten most abundant species of plants, herbivores and predators confirmed that beta diversity was higher for plants than for arthropods (Fig. 3-5). We registered 65 different plant species in the ten first ranks, in contrast to 34 herbivore species and 38 predator species (Fig. 3-5). These graphs also revealed that the patterns of dominance were highly variable among the cornfields. For plants, two cornfields had the most uneven distribution of abundances (e.g. A5 and F1, Fig. 3-5). This uneven distribution was due to the presence of invasive species such as *H. coronarium* and *G. sagittatum* whose cover values reached up to 71% and 45% of each cornfield. Herbivore communities also had uneven distributions of dominant species (Fig. 3-5b); the highest value of relative abundance was 46% and the four dominant species included two leafhoppers

(Cicadellidae), a leaf beetle (Chrysomeliade) and a katydid (Tettigonidae). Finally, predator communities had an uneven distribution of dominant species (Fig. 3-5c); the dominant species included flies from the families Dolichopodidae and Empididae, spiders from the genus Leucauge (Tetragnatidae) and ant species from the genera *Azteca*, *Linepithema*, *Brachymyrmex* and *Ectatomma* (Fig. 3-5c).

Figure 3-5. *Rank-abundance curves for the ten most abundant species of plants, herbivores and predators collected en twelve traditional cornfields (A1-A6 for cornfields mainly surrounded by human land-uses and F1-F6 for cornfields mainly surrounded by native forest in a radius of 250 m from its centroid). The lower-case letters in the curves represent only shared species among fields.*



The NMDS analysis indicated that dissimilarity in plant species composition was related to the landscape context in which the cornfield was located. Ellipses joining cornfields that were mainly surrounded by agricultural habitats (A1-A6) and cornfields mainly surrounded by native forest (F1-F2) conformed two distinct groups. This pattern was particularly evident when the similarity index was based on presence/absence data (Fig. 3-6a), whereas some overlapping occurred when the index favored common species (Fig. 3-6b). For herbivore species ($q = 0$) we observed a clear overlap in the composition of species between landscape contexts (Fig. 3-6c), whereas for abundant species ($q=2$) there was some degree of differentiation (Fig. 3-6d). Finally, we observed an overlap in species predator composition between landscape contexts (Fig. 3-6e-f). Therefore, the proportion of forest surrounding the crop did not have a substantial influence on the differentiation of arthropod communities among cornfields in the study area.

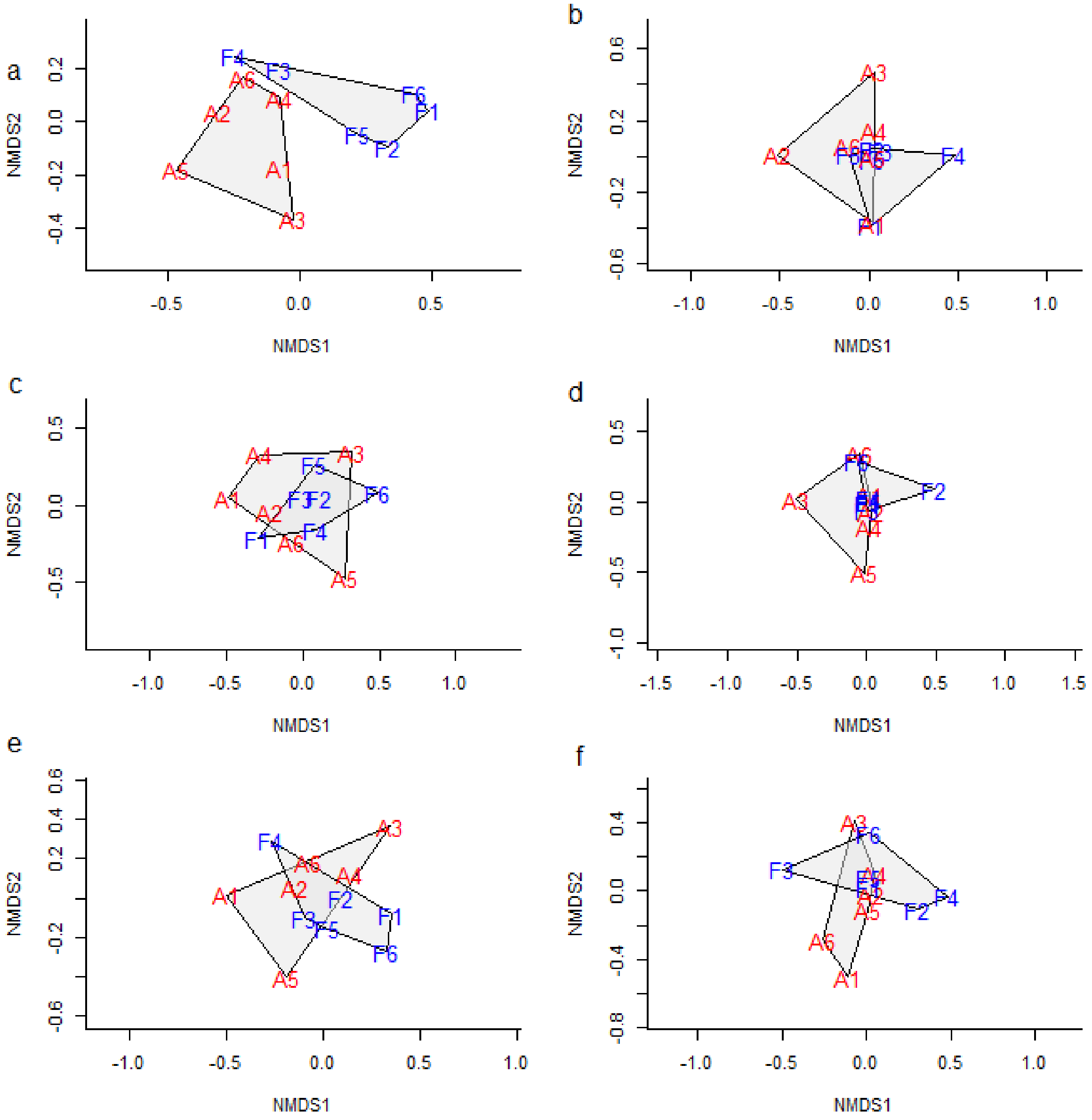


Figure 3-6.. Non-metric multidimensional scaling ordination diagrams based on the Jaccard (left column) and Morisita-Horn indexes (right column) for plants (a-b), herbivores (c-d), and predators (e-f) collected in twelve traditional cornfields. Capital letters represent cornfield codes: A1-A6 for cornfields mainly surrounded by human land-uses and F1-F6 for cornfields mainly surrounded by native forest in a radius of 250 m from its centroid. Ellipses indicate the clustering of biological communities based on the landscape context of the cornfield. Stress values: a = 0.01, b =0, c = 0.16, d=0, e=0.18 and f= 0.

Discussion

We determined that the amount of forest surrounding traditional cornfields is unrelated to the species richness of plants, herbivores and predators collected in those fields. Although we observed significant effects between the amount of forest and the diversity of the typical plants and abundant predators, we did not observe a clear trend in these data. Instead, other cornfield characteristics, such as the field's former land-use and the within-field diversity of typical plant species, were strongly related to diversity measurements. In particular, lower values of plant and predator diversities occurred in those fields previous to be sown with corn were invaded by a dominant plant. These results support a central role for local factors, such as crop management practices, in the assemblage of weed communities in crops. As discussed by Navas (2012), the structure of plant communities in agroecosystems depends on current conditions and the legacy of previous land use, because weeds can recover from the seed bank or through vegetative reproduction, after the destruction of plants in crop fields by agricultural practices. Therefore, the plant diversity in each field may reflect the composition and size of the seed bank, which in turn is mainly affected by field management (Franke *et al.* 2009).

Although no relationship was identified between the amount of forest around the crop and plant diversity, the results of NMDS analyses suggest that the closeness of cornfileds to forest do affect the composition of plant species. For instance, the dominant species in the agricultural context were *Pteridium aquilinum* (L.), *H. coronarium* and *Spermacoce* sp., whereas in the forest context the dominant species were *Impatiens balsamina* L., *Cortaderia* sp., *Brachiaria* sp. *Alocasia* sp. and *Drymaria cordata cordata* (L.) Willd. ex Schult. Therefore, future research should consider the impacts of landscape configuration and field management practices on not only on the diversity but also on the composition of the seed bank in crop fields.

Our results contrast with previous findings of a positive relationship between predator diversity and proximity to forest, in agroecosystems (Klein *et al.* 2006, Clough *et al.* 2009). Furthermore, when we analyzed the percentage of natural habitats surrounding the crop, our data did not support the hypothesis that non-cropped areas have a positive effect on the species richness of pest's natural enemies, in contrast to several previous studies (Clough *et al.* 2005, Schmidt *et al.* 2005, Schmidt *et al.* 2008). Therefore, predators in cornfields may be able to obtain resources, such as alternative prey, pollen and refuge in other anthropogenic habitats surrounding the field, including pastures and other crops. For example, the abundance of earwigs –a main predator of *Spodoptera frugiperda* J.E. Smith (Lepidoptera:Noctuidae) in maize crops-, was associated with higher cover of grassland habitats in the landscape, whereas spiders and ground beetles were more abundant in environments dominated by coffee plantations (Wyckhuys and O'Neil 2007). Clearly, further research is also needed to determine the role of habitat configuration and different land-use types on the population dynamics of a pest's natural enemies in crop systems.

Regardless of the order of diversity considered, we observed a strong and positive relationship between herbivorediversity and the diversity of common plant species in the cornfields.These results are consistent with the Plant Richness Hypothesis, which was initially formulated for galling insects and argues that the higher the number of plant species in a given site, the higher the number of herbivore species (Fernandes and Price 1988). Mechanisms explaining this relation may include higher host specialization by herbivores and the increase in plant species *per se*, if the number of herbivore species is similar among plant species but the number of plant species per area is higher (De Souza 2007, Lewinsohn and Roslin 2008). Becuase most phytophagous insect species (>70%) are specialized in their use of host plants (Price *et al.* 2011), the herbivores collected in cornfieds likely exhibit a high level of host specialization.

Contrary to our expectation of low species turnover among the twelve cornfields studied, we observed high beta diversity values, particularly for plants and predators in our study area. Dominant plant species were quite different among fields, which translated into high differentiation of plant communities. Predator communities also exhibited high turnover among the cornfields but differences in composition arose among rare species. Although, herbivore communities tended to be more homogeneous across cornfields, they also exhibited a high degree of differentiation. Our results support the idea of high turnover of weed species in agroecosystems (Navas 2012), as well as higher turnover of sessile organisms such as plants, in comparison with mobile species such as herbivores and predators (Jimenez-Valverde et al 2010). Similar findings of high beta diversity values for agroecosystems have been reported for weeds (Roschewitz *et al.* 2005) and arthropods (Clough *et al.* 2007) in temperate regions. Overall, these results indicate a high heterogeneity at small spatial scales, particularly if we take into account the small size of the study area (14 km^2). Such heterogeneity may be linked to the environmental gradients typical of mountain areas, landscape spatial configuration and crop management practices such as weeding and crop rotation. For instance, in mountainous environments it is possible to observe large changes in surface slope are possible at fine spatial scales, which in turn may affect soil properties, such as depth and water retention capacity, key factors for plant development (Western *et al.* 2002). In addition, plants can modify microhabitats through facilitating or inhibiting the colonization of other species (Callaway and Walker 1997), which in turn increases habitat heterogeneity, particularly because of the high number of species inhabiting traditional cornfields. Furthermore, if we consider plants as arthropod habitats, then plants deliver a high variety of resources and thus a higher number of potential niches, which also increases habitat heterogeneity, particularly for herbivores (Sobek *et al.* 2009, Price *et al.* 2011). This may explain why the turnover of herbivores was related to differences in plant richness among the cornfields.

We did not observe significant correlations between beta diversity matrices and environmental distance matrices for most groups of organisms. However, for herbivore communities, we observed that the higher the dissimilarity in the amount of surrounding forest, the higher the turnover of herbivores between cornfields. This result suggests that landscape configuration and, in particular, habitat patchiness may promote community differentiation through extinction-colonization dynamics (Jimenez-Valverde *et al.* 2010). Possible mechanisms explaining this result might include a reduction in the matrix permeability to the dispersal of organisms. For instance, some habitats can act as barriers to an organism’s movement, such as open pastures to understory birds (Sieving *et al.* 1996), or tall vegetation in crop borders to some wind-dispersed species like aphids (Fereres 2000). However, we did not find evidence for spatial autocorrelation in our data, and thus, mechanisms other than matrix impermeability and limited dispersal ability of organisms should be considered as factors explaining the high turnover of species among cornfields. Crop management practices at the local (in-field) and landscape scales, may contribute to beta diversity patterns by creating a mosaic of different disturbed patches (Limberger and Wickham 2012). Nonetheless, disturbances associated with crop management likely increase the productivity of the system, leading to high dominance of the fastest-growing species (Limberger and Wickham 2012), a pattern also observed in our data. By contrast, the high turnover of rare predator species might indicate that some species cannot remain in disturbed habitats, whereas, the dominant species might be agrobionts (Samu and Szinetár 2002). Thus, it remains unclear why so many plant species could dominate cornfields in this small sector of the landscape. We speculate that the number of plant species might be related to the composition of the seed bank and the land use history of the cornfields, which are factors that merit more attention in future research.

In summary, plant and arthropod diversity in traditional cornfields is not associated with a higher amount of native forest surrounding crop fields. However, the presence of forest may influence changes in plant species composition and turnover of herbivore communities among the cornfields. High habitat heterogeneity, derived from environmental gradients in mountain areas, high plant species richness, and high levels of disturbance associated with agricultural practices might be the most important factors explaining the high differentiation of plants and arthropods in cornfields. Moreover, the local distribution of plants has a substanbtial influence on the local distribution of herbivores, making this crop system ideal for developing better pest management strategies based on habitat manipulation (Isaacs *et al.* 2009, Landis *et al.* 2012a).

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4. The structure of arthropod-weed assemblages associated to traditional corn crops in the Colombian Andes

Abstract

Understanding the processes that shape biodiversity in agroecosystems is a key requirement for the design of strategies promoting the long-term sustainability of ecosystem services, such as food production, pest control and pollination.

We studied the organization of arthropod-weed assemblages in twelve traditional corn crops in the Colombian Andes. First, we investigated the effects of environmental factors on the structure of arthropod and plant metacommunities. Second, we described the architecture of species interaction networks.

The assemblages of plants associated to corn crops were significantly nested, i. e., species composition of cornfields holding fewer species are subsets of those fields holding more species. Altitude and content of organic carbon in soil were the most important factor accounting for the nestedness of plant assemblages, whereas the degree of forest cover surrounding the crops was the most important factor explaining the nestedness of arthropod assemblages. Only plant assemblages exhibited significant, albeit low modularity.

Species interaction networks were highly modular, with plants acting as module hubs and arthropods, particularly herbivores, being peripheral nodes. A strong modular structure of arthropod-plant interaction networks suggests that herbivores exhibit high specialization in host plant preferences. Forest cover in the landscape and weed richness within the cornfield influenced network size, the average number of links per species and modularity. Larger networks, more connected and less compartmentalized were observed in cornfields with larger forest cover around on them. Finally, network size affected herbivory and corn yield.

Our approach brings out the opportunity to study field and species traits that might be useful in ecological strategies for pest management. For example, our findings support the notion that increasing forest cover surrounding crops will rise the local diversity of herbivores' natural enemies and thus decrease the demand for the use of agrotoxicals. Additionally, the identification of few plant species working as module hubs in arthropod-plant interaction networks can provide useful information for the selective management targeting simultaneously weed and herbivore control.

Key words. -Agrobiodiversity, Herbivore Networks, land-use intensification, meta-community, modularity, nestedness.

Introduction

The challenge of supplying the growing global food demand and simultaneously reconciling agricultural production to environmental integrity requires a more in-depth understanding of the role that ecological interactions play in structure and functioning of agro-ecosystems (Robertson and Swinton 2005). Species interactions, such as pollination and natural control of pest crop populations, regulate agro-ecosystems functions that are critical to ensure food production (Memmott 2009). Empirical studies suggest that more diverse assemblages of pest's natural enemies may enhance biological control in crops (Symondson *et al.* 2002, Bianchi *et al.* 2006), as well as, that pest's natural enemies are more abundant and diverse in complex landscapes, e.g. those with larger percentage of natural and semi-natural habitats (Bianchi *et al.* 2006, Chaplin-Kramer *et al.* 2011). However, agroecosystems with diverse assemblages of herbivores and their natural enemies may have reduced pest control as a consequence of intraguild predation and apparent competition between herbivores (Thies *et al.* 2005, Bohan *et al.* 2013, Martin *et al.* 2013). Therefore, a classical approach to evaluate pest control based on measurements of species richness or abundance of arthropods has limitations understanding the mechanisms through which biodiversity improves pest regulation in agroecosystems.

As an alternative, the study of ecological interactions between species in crops may solve that problem by identifying keystones species or functional groups that contribute to the ecological function, as well as to the stability and resilience of agroecosystems (Bohan *et al.* 2013). Previous research in agroecosystems has explored the effects of land-use intensification on species interactions, as well as, in their associated ecological functions. For example, comparisons of networks structure between organic and conventional farming confirmed more diverse assemblages of plants and arthropods, as along with, more stables rates of parasitism under organic management (Macfadyen *et al.* 2009, Macfadyen *et al.* 2011a). Likewise, in intensively managed agricultural habitats most energy flows along one or few pathways (Tylianakis *et al.* 2007), and modularity may increase (Macfadyen *et al.* 2011b). However, not always a complex landscape is associated with a more complex network structure, for example a lower complexity was reported for aphid-parasitoid interactions in complex landscapes (Gagic *et al.* 2011), due to higher dominance of one species of aphid in such landscape. Thus, more research is needed to understand the impacts of land-use intensification and particularly, landscape simplification on ecological network structure in agroecosystems.

Additionaly, network analysis is being used to evaluate how the robustness of interaction networks -a measure of network's vulnerability to species loss- varies across gradients of land use intensification and among different types of networks present in agroecosystems. From these studies it is known that aphid, insect seed feeder, and pollinator networks appeared more fragile to local extinction of species (Pocock *et al.* 2012), whereas in host-parasitoids networks empirical evidence does not support the idea that land-use intensification influences negatively the robustness of ecological networks (Macfadyen *et al.* 2011b). However, these conclusions have been drawn from few studies in temperate regions, and little is known from network structure in tropical agroecosystems.

Given that ecological processes that affect diversity in agricultural landscape operate at higher spatial scales than crop fields (Tscharntke *et al.* 2012), we must consider several spatial scales for evaluating patterns in diversity in agricultural landscapes. As crop fields are discrete habitats in the landscape, with particular assemblages of species and territories beyond field limits, we could apply the concept of metacommunity –a set of local communities that are linked by dispersal of multiple potentially interacting species (Leibold *et al.* 2004)– to analyze the organization of plant and arthropod communities across the landscape in relation to environmental gradients in agroecosystems.

Metacommunities could exhibit nestedness and/or modularity. Nestedness merges when species composition of crop fields holding fewer species are subsets of those fields holding more species, whereas modularity reflects the tendency for species to replace each other from site to site (Leibold and Mikkelson 2002). Identifying these patterns allows us to recognize which species are more sensitive to habitat fragmentation, as well as, to understand how species respond to environmental gradients. This information is useful to design strategies for conserving biodiversity, e.g. a single large area if metacommunities are nested or several smaller areas if they are compartmentalized (Mendez 2004).

Here we address these issues by studying the organization of arthropod-weed assemblages in traditional corn crops in the Colombian Andes. First, we investigated the effects of forest cover and other environmental factors on the structure of arthropod and plant metacommunities. Second, we described the architecture of species interaction networks and their relationships with forest cover and ecosystem functioning. We addressed the following questions: *i) H*ow are plant and arthropod communities organized across the studied landscape? *ii)* To what extent is the organization of these communities influenced by environmental factors and forest cover in the landscape? *iii)* How does the structure of weed-arthropods networks change across a gradient of forest cover and other environmental factors? *iv*) To what extent are herbivory and crop yield affected by arthropod-weed network structure?

We predict that organization of species across the landscape respond to ecological processes, thus the structure of metacommunities will not be random, and forest cover in the landscape will be a major factor explaining such patterns. We also expect the cover of forest in the landscape to affect the structure of arthropod-weed networks in cornfields; then we expect a more complex network structure in cornfields with larger cover of forest around on them. Finally we expect less damage in corn plants and a higher production as the arthropod-weed networks become more complex.

This work improved our understanding of interactions that occur in complex agroecosystems, as well as their relationships with provision of ecosystem services. Such information is useful to manipulate agroecosystems in order to achieve a sustainable intensification of agriculture.

Material and Methods

Description of study area and environmental descriptors of cornfields were provided in the section of materials and methods in chapter 2. Similarly, sampling of arthropod and weed data for meta-community analysis, as well as, measruments of herbivory and crop yield were described in chapter 2.

Co-occurrences of arthropod and plant species. On September 2011, we performed five manual sampling events for each study site. In each sampling event, all arthropods found on maize plants were collected during 5 minutes by two people. On December 2011, we sampled the arthropods species occurring on the three dominant weeds for each maize field, following the former procedure and taking five manual-collecting samples per plant species. A total of 20 hours of observations were accumulated in both sampling dates.

Data analyses. We used incidence matrices to construct species accumulation curves in Estimates 8.2 (Colwell 2009). To determine if the sampling effort was sufficient to characterize arthropods and plants communities colonizing maize fields, we used the completeness of the non-parametric estimator ICE (Colwell 2009). A Pearson Product Moment Correlation Test was conducted to determine association among environmental and field traits, in order to select only independent variables for further analysis. We defined a significance level of 0.05.

To describe the distribution of arthropod and weed species through the cornfields, we constructed incidence matrices in which localities correspond to rows and species to columns. We computed nestedness for each incidence matrix using the NODF index (Almeida-Neto *et al.* 2008) for rows. To determine if observed nestedness departs from values expected under randomness, we used the null model 2 presented in Bascompte *et al.* 2003., in which the probability of presence of a specie in a determinate site is proportional to the total number of species presents in all sites. We ran 100 simulations to report *P*-values representing the probability of the observed nestedness overlaping the distribution of nestedness values generated by the null model. The nestedness analyses were performed in the software ANINHADO version 3.0 (Guimarães & Guimarães, 2006) with ordered matrices.

To identify environmental factors or field traits that can account for nestedness, we re-ordered the rows (localities) in the incidence matrices according to altitude, field size, the proportion of forest cover in a radius of 250 m from the center of each crop, the percentage of organic carbon in the soil, and plant species richness. Except for altitude, all factors were ordered in a decreasing way. Thus we computed nestedness using ANINHADO to calculate NODF values without ordering the matrix. In order to get an error measure for NODF's values, we used a resampling Jacknife procedure implemented in the R (R_Development_Core_Team 2008) to obtain 95% confidence intervals, assuming a normal distribution of NODF's values.

To evaluate the degree of compartmentalization in incidence matrices, we computed modularity (M) using the software Modular version Alfa 0.1 (Marquitti *et al.* 2012). We applied the method of Barber available in Modular to maximize M, and used a number of 100 simulations to contrast observed M-values with a null model.

Arthropods – plants network topology. We constructed bipartite networks for each cornfield and calculated the following network structure descriptors: network size, connectance, average number of links per species, nestedness, number of compartments and modularity. Network size was defined as the total richness of arthropod species. Connectance was calculated as the fraction of recorded interactions relative to the total possible interactions. The average number of links per species was used as a measure of cohesion of the network. Nestedness, a topological pattern in which species with fewer interactions are preferentially associated with a subset of species that interact with the most connected ones (Bascompte *et al.* 2003), was calculated with the nested overlap and decreasing fill (NODF) metric, using the software ANINHADO. The significance of this metric was estimated with a Monte Carlo procedure, performing 100 randomizations created from the null model two (Bascompte et al 2003), in which the probability of an interaction between a plant and an animal is proportional to the total observed number of their interactions. Finally, we tested the networks for modularity, an ecological pattern that occurs when a group of species interact more often with species within the group than with the rest of the species in the network (Krause *et al.* 2003, Lewinsohn *et al.* 2006, Guimerà *et al.* 2010). Modularity was estimated by using the index M from the software Modular, version Alfa 0.1 (Marquitti *et al.* 2012), based on the algorithm of Barber, while its significance was estimated using a Monte Carlo procedure created by the null model two presented in Bascompte *et al.* (2003). To carry on comparisons among networks from different cornfields, standardized modularity (M’) was calculated as

$$M' = (M - M_{null\ model})/M_{null\ model}$$

Where M is the value of modularity of the current matrix, while $M_{null\ model}$ refers to the average value of modularity of the random replicates. Graphs depicting the ecological interaction networks were built using Ucinet, version 6.414 (Borgatti *et al.* 2002).

We used Poisson log-link Regression and Ordinary Least Square Regression (OLS) to analyze changes in network size, links per species, and relative modularity in relation to the proportion of forest in a radius of 250m around each cornfield. Field size, altitude and plant species richness were included in the models as covariates. Similarly, regression models were used to assess the relationships within network's metrics and foliar herbivory and crop yield.

In all cases we used stepwise forward simplification for model specification in order to comply with the principle of parsimony (Crawley 2003). To control possible multicollinearity among predictors we calculated the Condition Number and the Variance Inflation Factor (Chen *et al.* 2003). Outliers and influential points were identified graphically by plotting normalized residuals squared against leverage (Chen *et al.* 2003). Points with the largest leverage and the largest residual square were checked before to define the models. Constant error variance was checked by plotting the standardized residuals against fitted values, while normality of residuals was checked graphically plotting residuals and fitted values (Crawley 2003). Independence in residuals was evaluated with a Durbin-Watson's Test (Chen *et al.* 2003). All the analyses were conducted using R software (R_Development_Core_Team 2008).

Results

Plant species richness and composition. The richness of plants associated to traditional maize fields in Topaipí totalized 198 species distributed in 29 orders and 53 families. Most species belong to the classes Magnoliopsida (70.2%), Liliopsida (24.7%), and Polypodiopsida (4.5%). With regards to growth forms, there was a prevalence of herbaceous plants (69.7%), although vines (9.1%), shrubs (7.6%), dwarf shrubs (6.6%), ferns (4.5%) and re-growth of trees (2.5%) were also present. According to measures of relative coverage and frequency, the weeds *Drymaria cordata cordata* (L.= Willd. Ex Schult (Caryophylaceae) and *Spermacoce assurgens* Ruiz & Pav. (Rubiaceae) dominated the plant assemblages associated to traditional maize fields. Other specie recurrently observed in the study sites were Impatiens sp. (Balsaminaceae), *Cyperus luzulae* (L.) Rottb. Ex Retz.. (Cyperaceae), *Commelina erecta* L. (Commelinaceae), *Panicum* sp. (Poaceae) and *Sida rhombifolia* L. (Malvaceae). On the other hand, invasive species as *Pteridium aquilinum* (L.) Kuhn (Dennstaedtiaceae), *Hedychium coronarium* Koenig (Zingiberaceae), *Brachiaria* sp. (Poaceae) and *Impatiens balsamina* L. . (Balsaminaceae) had the higher values of coverage.

Arthropod species richness and composition Our samples totalized 10.662 individuals of arthropods distributed in nine orders and 125 families. Most specimens were herbivores (66.7%), followed by predators (17.9%) and parasitoids (12.6%). Cicadellidae (Hemiptera) and Chrysomelidae (Coleoptera) were the most abundant families among herbivores. Formicidae (Hymenoptera), Dolichopodidae (Diptera) and Araneidae (Araneae) were the most abundant taxa among predators, whereas Braconidae and Pteromalidae (Hymenoptera) were the most abundant families among parasitoids. The most diverse groups were herbivores and predators with 260 and 152 morphospecies, respectively. However, we did not determine the morphospecies of parasitoids and saprophagous.

Meta-community structure. Table 4-1 summarizes the structure of weed and arthropod assemblages associated to traditional maize crops. The local assemblages of herbivores, predators and total arthropods exhibited higher nestedness than it would be expected by chance. However, modularity did not differ from values expected by chance for all arthropod trophic groups. Weed assemblages are significantly and highly nested and present a low, albeit significant, degree of modularity.

Reordering the incidence matrices according to environmental gradients unraveled the effects of field traits on metacommunity structure. For weeds, altitude and the percentage of carbon in soil were the most important environmental variables affecting observed nestedness (Fig. 4-1). Other factors, such as field size and the percentage of surrounding forest cover also explained the nestedness in weed composition. For herbivores and total arthropods, the most important factor affecting nestedness was the number of weed species (Fig. 4-1 b & c), whereas the percentage of surrounding forest cover was the most important environmental factor affecting nestedness of predator assemblages (Fig. 4-1d).

Table 4-1. Summary statistics for indices of nestedness (NODFrows) and Modularity calculated for weed and arthropod species composition in twelve corn fields. Values for NODFrows and Modularity from null models were averaged from 100 randomization simulations ± one standard deviation. P-values represent the probability that the observed value came from the same distribution of null models.

Group	Nestedness	Modularity

	NODFrows$_{obs}$	NODFrows$_{null}$	P-value	Modularity $_{obs}$	Modularity $_{null}$	P-value
Plants	44.58	32.10 ± 1.68	<0.001	0.33	0.29 ± 0.01	<0.001
Herbivores	61.59	40.79 ± 1.45	<0.001	0.21	0.21 ± 0.01	~1
Predators	43.66	30.78 ± 2.23	0.02	0.29	0.29 ± 0.01	0.85
Total Arthropods	56.35	38.16 ± 1.27	<0.001	0.22	0.23 ±0.01	~1

Weed-arthropod interaction networks. We registered 264 species of arthropods interacting with 24 weed species along the twelve studied cornfields. Most species were herbivores (154 morpho-species, 58.3%) and predators (75 morpho-species, 28.4%). Table 4-2 summarizes the structure of matrices describing the co-occurrence of arthropods and weeds –used here as proxy for the local ecological interaction networks–.

Both plant richness within cornfields and the proportion of forest in a radius of 250 m around on each cornfield had positive relationships with the size of the arthropod-weed networks, but only predator richness did not respond to changes in plant richness (Fig. 4-2 a-f). Additional environmental descriptors of cornfields, such as altitude and field size, were unrelated to changes in arthropod species richness regardless the trophic group considered (Fig. 2 g-l see Appendix 4-1).

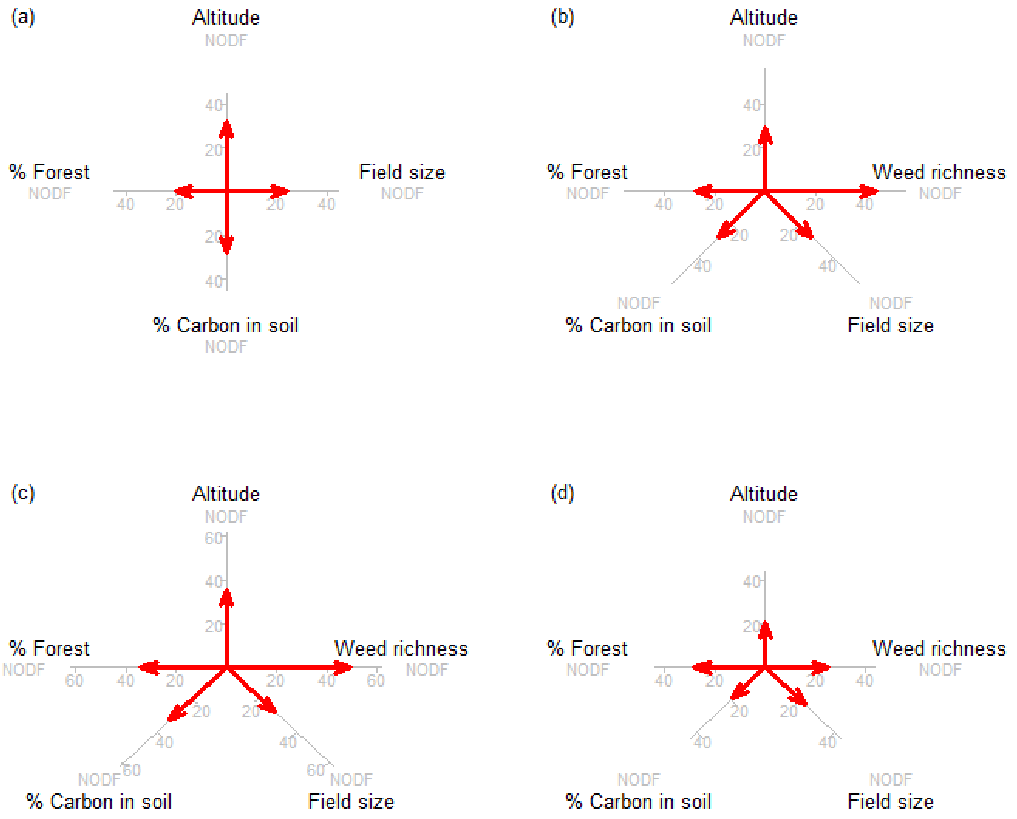

Figure 4-1 Contribution of environmental gradients to nestedness in Plants (a), Total arthropods (b), Herbivores (c) and Predators communities (d), studied in twelve traditional cornfields in the Colombian Andes. In each plot, the axis represent the maximum. observed value of nestedness, while arrows indicates the value of nestedeness calculated from an incidence matrix, in which sites were ordered following gradients in altitude, field size, forest cover in the landscape, content of organic carbon in soil and weed richness (only for arthropods).

The interaction matrices were not significantly nested but highly compartmentalized (Table 4-2). The number of identified modules corresponds to the number of weeds species sampled in each field, as observed in the respective graphs (Fig. 4-3). Connectance values ranged from 0.29 to 0.40 and were unrelated to network size (Pearson's r test = -0.18, p = 0.56). The average number of links per species was 1.19 ± 0.08 and it had a positive relationship with the proportion of forest around cornfields (Fig. 4-4a). In contrast, the standardized values of modularity were negatively related to forest cover in the landscape (Fig. 4-4b, Appendix 4-1).

Table 4-2. *Structure network's metrics for arthropod-weed assemblages collected in twelve traditional cornfields in the Colombian Andes.*

Cornfield code	Connectance (C)	Average links per specie	Nestedness (NODF)	Modularity (M)	Standardized modularity
A1	0.30	1.10	67.21	0.59	0.31
A2	0.29	1.05	61.99	0.61	0.30
A3	0.32	1.17	43.74	0.54	0.23
A4	0.32	1.22	53.91	0.53	0.26
A5	0.33	1.21	46.02	0.52	0.25
A6	0.31	1.13	58.23	0.56	0.27
F1	0.40	1.09	49.07	0.49	0.22
F2	0.35	1.30	48.62	0.47	0.19
F3	0.33	1.23	59.19	0.52	0.24
F4	0.34	1.28	58.24	0.49	0.23
F5	0.32	1.20	51.42	0.53	0.23
F6	0.35	1.30	53.67	0.47	0.21

Network size influenced foliar herbivory and crop yield. Particularly, herbivore richness had a positive and significant relationship with herbivory (Fig. 4-5a, Appendix 4-2), while predator richness was positively related to crop yield (Fig. 4-5b, Appendix 4-3). Other network's metrics such as connectace, average links per species and modularity were unrelated to herbivory or corn production in the studied cornfields.

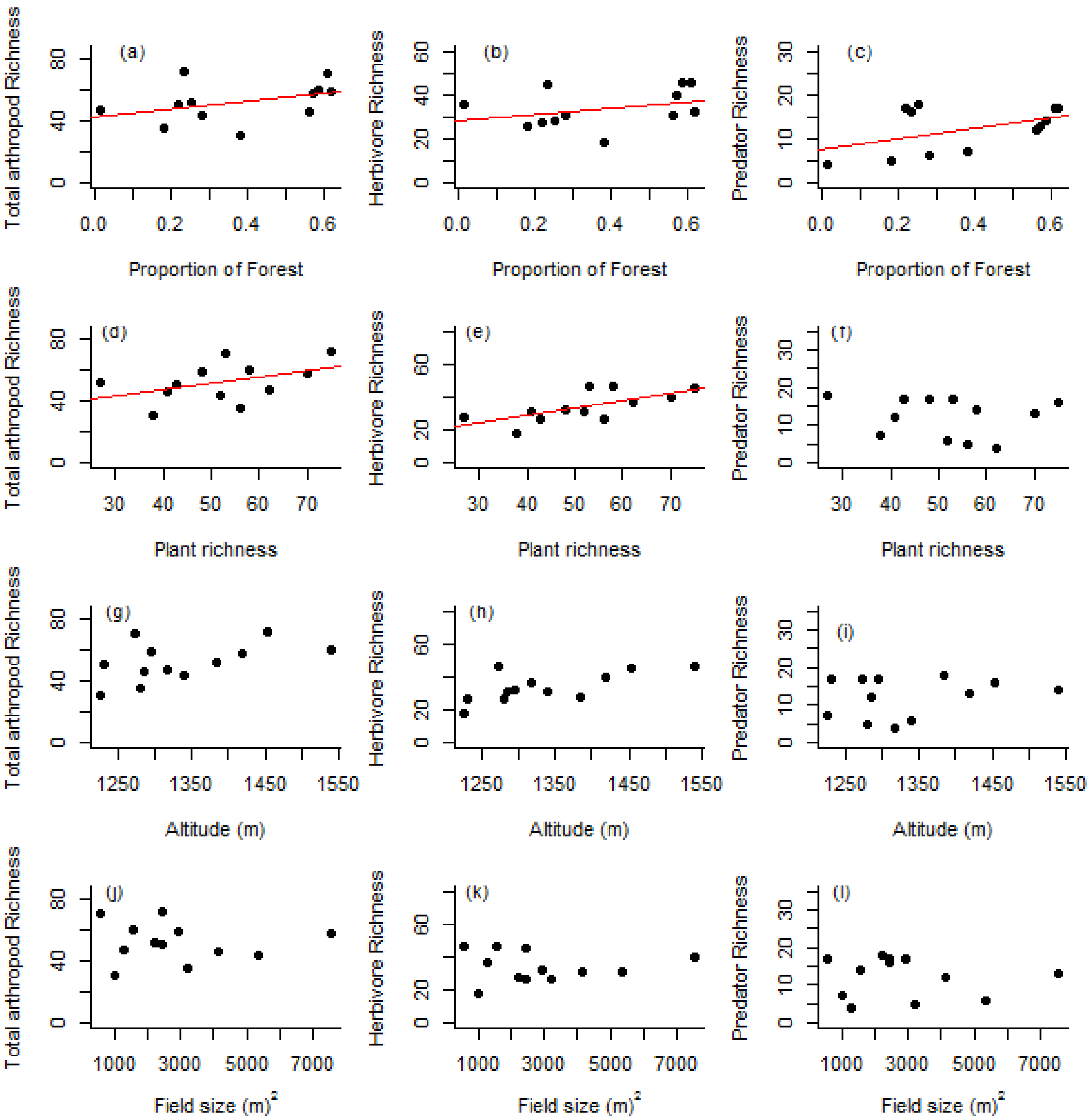

Figure 4-2.. Variation in network size defined as the total richness of arthropods (a, b & c), herbivore richness (d, e & f) and predator richness (g, h, & i) in relation to changes in the proportion of forest in a 250m radius around on each cornfield (a, d & g), altitude (b, e & h) and field size (c, f & i). Lines indicates predicted values of Poisson regression models and only were plotted when the factor was significant at a confidence level of 95%.

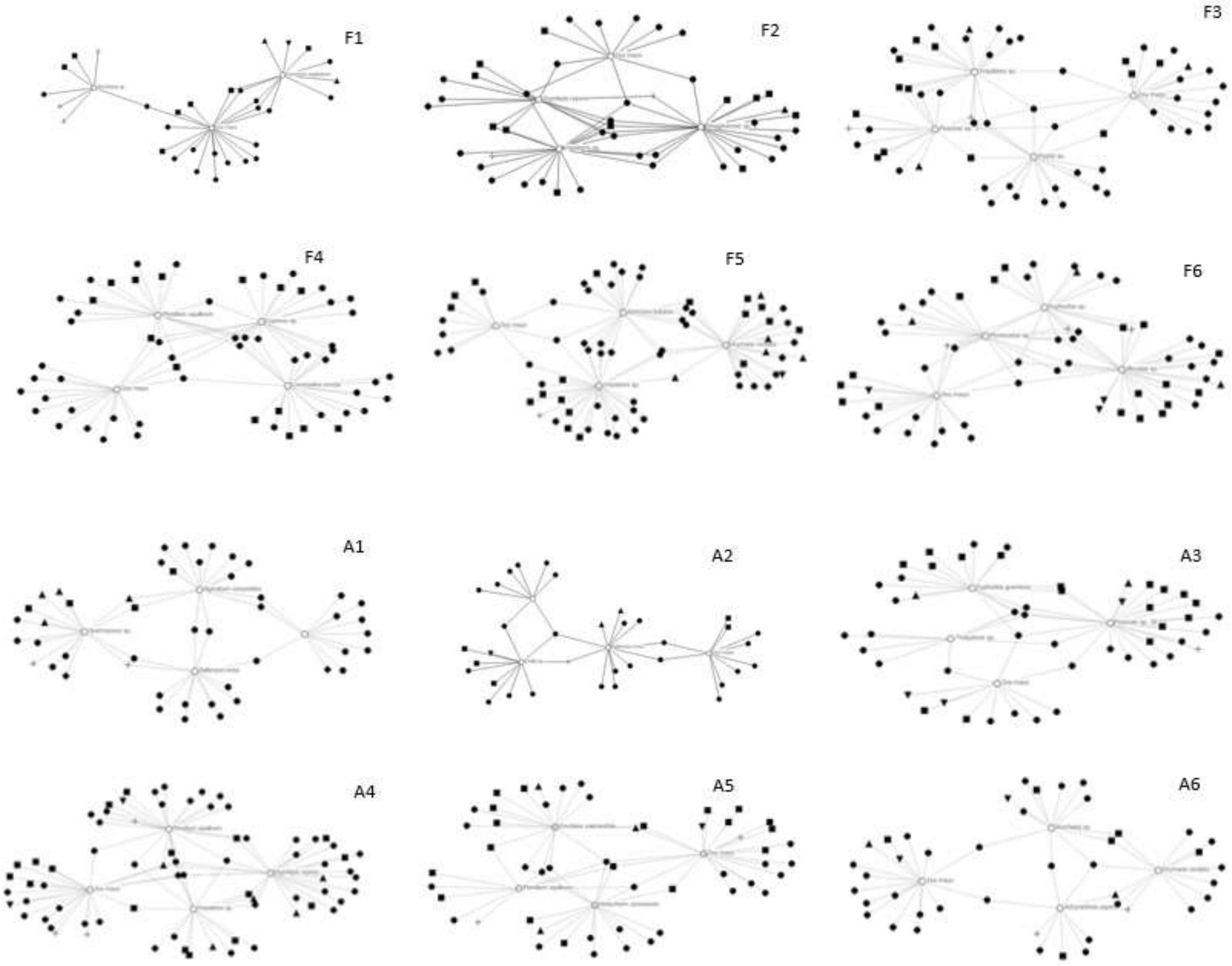

Figure 4-3. *Modular structures from weeds and arthropod co-occurrence networks for each corn field. Corn plants and the three dominant weeds in each field were inspected for arthropods. Plant species were represented by white circles, herbivores by black circles, predators by squares, pollinators by plus, parasitoids by up triangles and saprophagous morphospecies by down triangles. Farm codes were in the upper right corner of each graph.*

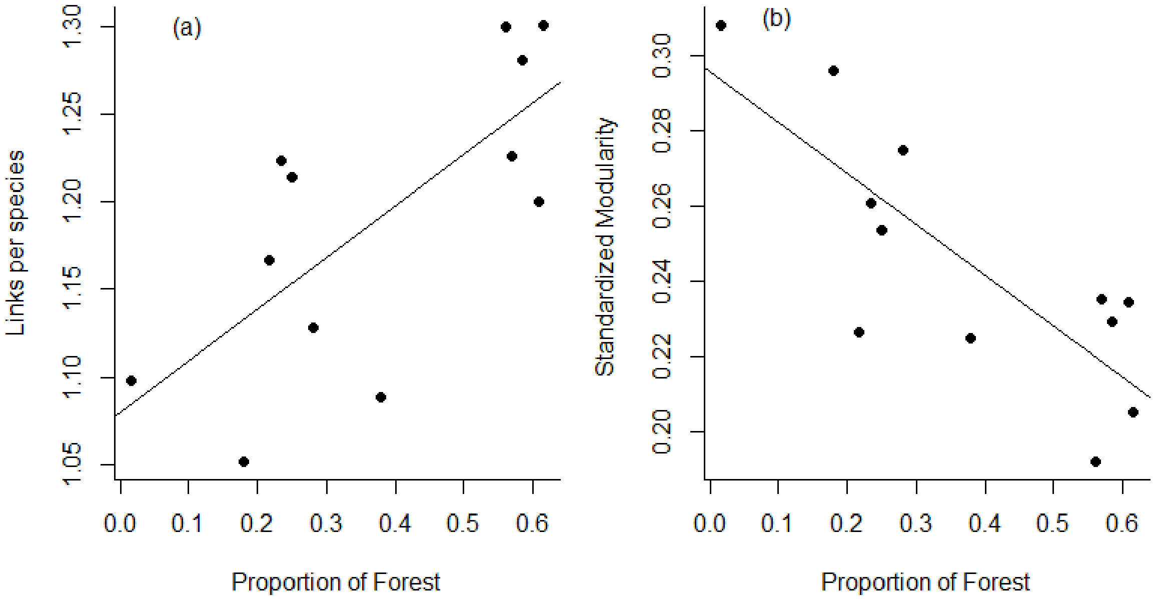

Figure 4-4 Average number of links per species (a) and Standardized Modularity in relation to the proportion of native forest in a radius of 250m around of each crop field measured on arthropod-weed interactions networks in traditional cornfields in the Colombian Andes.

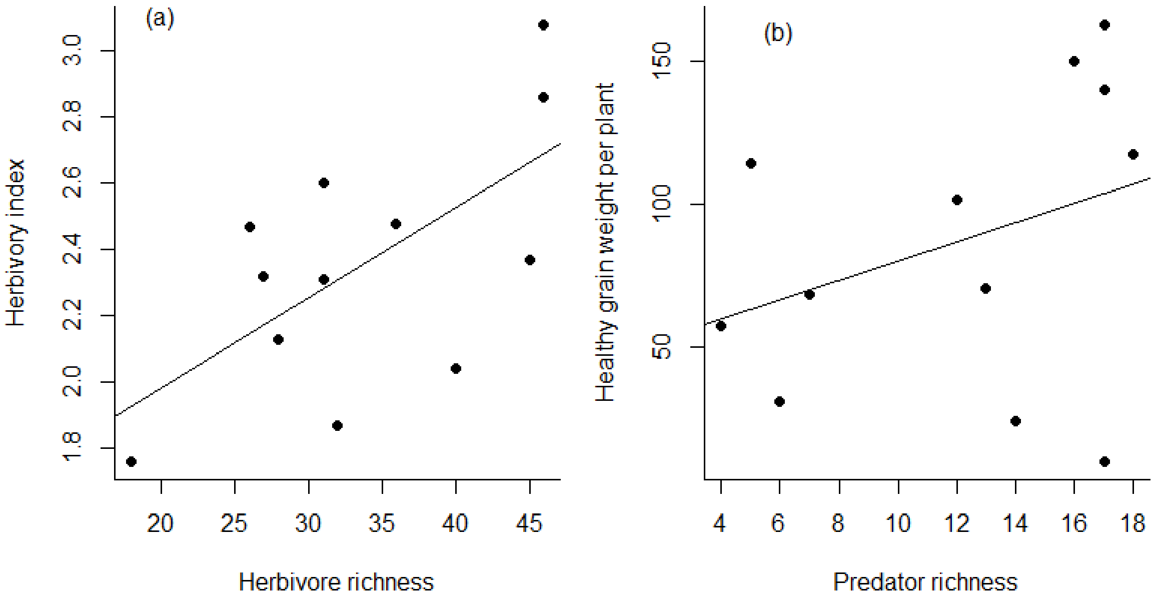

Figure 4-5 Relationship between herbivory index and herbivore richness (a) and between crop yield and predator richness (b), measured in arthropod-weeds interaction networks in twelve traditional cornfields in the Colombian Andes.

Discussion

Plant and arthropod assemblages in the studied agricultural landscape had a nested structure, which means that species composition of cornfields holding fewer species are subsets of those fields holding more species. Altitude and the content of organic carbon in soils were the most important factors accounting for the nestedness of plant assemblages, whereas the degree of forest cover surrounding the crops and plant richness were the most important factors explaining the nestedness of arthropod assemblages. Only plant assemblages exhibited significant, albeit low modularity.

These results suggest that colonization of cornfields by plant species may depend more on local characteristics and crop management practices than on landscape configuration. For instance, the content of organic carbon in soil is highly dependent on management practices such as tillage, land preparation for sown, (e.g. Slash and burn, mulch or weeding with glyphosate) and fertilization, which are recognized factors influencing community structure of weeds in agricultural landscapes (Navas 2012). Plant assemblages were more diverse at higher altitudes, however when we considered previous land-use of plots in analysis explaining plant species richness, the importance of altitude as explaining factor diminished, whereas former land-uses such as pastures or previously invaded plots accounts for most reduction on plant diversity (EMP, unpublished data). Therefore, further research should address the effect of biological invasions on seed banks in agricultural fields and their impact on plant community assemblage.

Nevertheless, a significant but low modularity in plant assemblages may indicate a high turnover of species across the landscape, what was demonstrated in previous analysis of beta diversity in the same data (EMP, Unpublished data). It suggests that habitat heterogeneity is high in the studied landscape, and even more importantly, that the negative impacts of agricultural intensification through transformation of forest in croplands in biological communities (e.g. homogenization of communities) occurs at larger spatial scales than the one we considered here.

In regard to nestedness in herbivore and predator assemblages, our results support the idea that plant richness is the main factor explaining herbivore richness (Lewinsohn and Roslin 2008), and also that natural habitats, like forest cover in the landscape, are related to higher diversity of predator assemblages in crops (Bianchi *et al.* 2006, Klein *et al.* 2006, Chaplin-Kramer *et al.* 2011). Differences in plant species compositions across cornfields in the landscape also may explain nestedness in herbivore assemblages, given that most phytophagous insects have specific associations with their host plants (Novotny and Basset 2005).

Nested patterns in predator composition related to gradients in forest cover in the landscape could indicate that the presence of permanent habitats from which predators can spill-over onto other habitats would be determining of crop natural enemies assemblages in crops (Klein *et al.* 2006, Holzschuh *et al.* 2009, Tscharntke *et al.* 2012). For example, the presence of forests could be shelter for predators in the seasons in which the crop is not present or is subject to disturbance, such as weeding or harvesting (Klein *et al.* 2006). Moreover, for predators, the supply of alternative prey habitats and extra resources such as nectar and pollen, or refuges in proximity of natural habitats can improve habitat suitability (Isaacs *et al.* 2009, Landis *et al.* 2012a, Rusch *et al.* 2013b).

Even though the relation between nestedness and gradients in environmental factors evaluated helps to improve our understanding of mechanisms that explain the distribution patterns of the species in the agro-landscape, further research should consider that species in agroecosystems exploit resources in different habitats (Fahrig *et al.* 2011b, Tscharntke *et al.* 2012). Therefore, we must take into account habitat suitability of different land-uses and covers in the landscape, as well as, the permeability of the matrix of landscape to species dispersion (Hadley and Betts 2012). In this way, we could assess how habitat loss affect community assemblages and ecological functions in agroecosystems.

The network of species co-occurrences between weeds and arthropods in cornfields were highly modular with only a few plant species structuring arthropod assemblages. Dominant weeds in each corn field acted as a module hub, which were connected to a number of peripheral nodes conformed by arthropods.

Our results are consistent with the expectation that antagonistic networks, such as herbivore-plant or prey-predator tend to be more compartmentalized (Prado and Lewinsohn 2004, Guimaraes *et al.* 2006). Similar results, reporting high modularity in herbivory networks, have been shown both in natural ecosystems (Prado and Lewinsohn 2004, Cagnolo *et al.* 2011) and agricultural contexts (Macfadyen *et al.* 2011b). However, modularity is not restricted to antagonistic interactions, and it has also been reported for mutualistic networks like plant-pollinators (Olesen *et al.* 2007, Dupont and Olesen 2009, Martín González *et al.* 2012), seed-dispersers (Donatti *et al.* 2011, Mello *et al.* 2011) and ant-plants (Fonseca and Ganade 1996, Guimaraes *et al.* 2007, Dáttilo *et al.* 2013).

A possible explanation for compartments in our network may include high specialization in host preferences by herbivores (Prado and Lewinsohn 2004). According to a previous review on host specificity in herbivore communities (Novotny and Basset 2005), we could expect the proportion of herbivores feeding on a single plant species, and hence specialization, to increase as the taxonomic dissimilarity in plant species composition also increases in the community. In fact, in most of the corn fields studied (nine out of twelve), weeds species belonged to different plant families, which could promote differences in the composition of herbivore assemblage for each plant and hence modularity. Some ecological constraints to species interactions imposed by plant defenses and detoxification mechanisms in their counterparts herbivores also might shape herbivores assemblages (Agrawal 1998, Kareiva 1999, Ohgushi 2005) and compartmentalized plant –herbivore networks (Cagnolo *et al.* 2011). On the other hand, we need to explore if modules in our network are composed by closely taxonomic related species of herbivores. If that is true, modules can be the result of a phylogenetic signal (Rezende *et al.* 2009, Guimerà *et al.* 2010). However, our scarce knowledge of tropical insect's taxonomy and their host specificity, limit us in our understanding of the relative importance of different mechanism as a determinants of compartmentalization in ecological networks. In addition, other factor as phenology (Martín González *et al.* 2012), habitat preferences (Guimerà *et al.* 2010), and the role of different species in the networks (Dupont and Olesen 2009) needs to be considered.

In regard to the question of how forest cover affects the structure of arthropod-weed network our result supports the idea that simplification of landscape through land clearing simplify network structure. For instance, we observed higher links per species, as well as, larger network size in cornfields with larger forest cover around them, but modularity had a negative relationship with changes in forest cover. Then, these findings support the idea that agriculture most often produces compartmentalized food webs (Macfadyen *et al.* 2011b, Bohan *et al.* 2013), and in this case increasing modularity may indicate that the destruction of forest in the agricultural landscape is leading to the fragmentation of food webs in cornfields (Guimerà *et al.* 2010).

Finally, we observed that network's metrics were related to ecological functions such as herbivory and yield crop in the studied cornfields. Herbivory was higher in cornfields with more species of herbivores in the network. However, production of corn was higher in cornfields that hold networks with more predator species. These results support the hypothesis that more diverse assemblages of predator's enhance biological pest control in crops by increasing complementarity of predator species in regulating populations of herbivores (Bohan *et al.* 2013). However, complementarity among herbivore species may lead to higher herbivore in crops with negative consequences for crop yield (EMP Unpublished data).

To sum up, in complex agroecosystems such as the traditional cornfield studied, forest cover in the landscape and plant diversity play a central role in structuring assemblages of species in the landscape as well as in structuring arthropod-weed networks in each cornfield. We conclude that landscape simplification reduces species diversity arthropods in cornfields and it may lead to fragmentation of arthropod-weed food webs. The structure of these food-webs influences crop production: on one hand more diverse predator assemblages favor pest regulation, on the other hand more diverse assemblages of herbivores increases herbivore pressure on crops.

Our findings support the notion that increase of forest cover surrounding crops will increase the local diversity of herbivores' natural enemies and thus decrease the demand for the use of agrotoxicals. Additionally, the identification of few plant species working as module hubs in arthropod-plant interaction networks can provide useful information for the selective management targeting simultaneously weed and herbivore control.

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5. Landscape simplification and weed diversity affect pest control and production in Andean traditional cornfields

Abstract

Land clearing increases landscape simplification and threats biodiversity and ecosystem service provision in agroecosystems. However, the evidence of detrimental effects of landscape simplification on biodiversity and pest control is scarce in complex agroecosystems such as tropical traditional crop systems.

We studied the relationships between forest cover, weed and arthropod diversity, herbivory and crop production in twelve traditional cornfields in the Colombian Andes. The cornfields were located in a gradient of forest cover within a radius of 250 m around on them, which enabled us to assess changes in diversity related to this factor. We also evaluated the effects of other covariates such as soil organic matter, previous former land-use and perimeter-to-area ratio of cornfields.

Forest cover had positive relationships with the coverage of weeds and the richness of leaf-chewer herbivores. However, the proportion of forest was related negatively to the abundance of sap-feeder herbivores and parasitoids.

Plant richness within cornfields enhances the abundance of natural enemies, particularly of parasitoids. Whereas the richness of grasses was associated to lower infestation levels by whorl worms. Richness and coverage of plants responded to changes in soil organic matter and previous use of cornfields.

Corn production had a negative relationship with foliar herbivory, which in turn was positively related to the richness of leaf-chewer herbivores.

Plant diversity had an indirect positive effect on corn production, by enhancing the abundance of natural enemies and pest control in cornfields. Whereas forest may negatively affect indirectly corn yield by enhancing the richness of leaf-chewer herbivores and herbivory in the studied crops. This apparently “dis-services” of forest in pest control need to be considered with caution, because forest in agricultural landscapes are essential for the provision of additional ecosystems services, that should be taken into account to have an accurately assessment of their role in sustainable agriculture.

Key Words: Zea mays, conservational pest control, associational resistance, enemies hypothesis, agrobiodiversity, weeds, herbivory, traditional crops.

Introduction

Remnants of native forests in agricultural landscapes provide valuable ecosystem services to society; they can minimize flooding, moderate regional climate, remove and store atmospheric carbon dioxide and enhance pest regulation in crops (Tilman *et al.* 2002, Klein *et al.* 2006). However, the growing demand for agricultural land prompts the conversion of more natural habitats into croplands with serious long-term implications for the environment (Tilman *et al.* 2011). For instance, habitat destruction is the major cause of biodiversity loss (Dirzo and Raven 2003), whilst simplification of the agricultural landscape through land clearing is leading to a higher pest pressure on crops (Poveda *et al.* 2012), lower abundance of natural enemies and less pest control in agroecosystems (Bianchi *et al.* 2006, Chaplin-Kramer *et al.* 2011)

The availability of natural habitats in agricultural landscapes is critical for conservative pest control (Gurr *et al.* 2003b, Tscharntke *et al.* 2012, Rusch *et al.* 2013a). Empirical evidence suggests that natural and semi-natural habitats embedded in agroecosystems maintain the regional pool of species of beneficial arthropods (Schmidt *et al.* 2005, Schmidt and Tscharntke 2005, Klein *et al.* 2006, Pluess *et al.* 2010, Chaplin-Kramer *et al.* 2011, Letourneau *et al.* 2012b). Some mechanisms have been proposed to explain these relationships. For instance, natural habitats are permanent covers, where beneficial arthropods can built-up larger populations without disturbance (Klein *et al.* 2006); these habitats exhibit a source-sink dynamic, serving as a source habitat for arthropods in the initial colonization of the crop fields (Schuepp *et al.* 2011), and as a sink habitats when the management practices force them to abandon the crop fields (Rand *et al.* 2006)

Better pest suppression in complex landscapes may occur due to higher plant diversity. For instance, the ‘enemies hypothesis’ predicts that natural enemies will increase in diversified agroecosystems and thereby control herbivores more effectively (Risch 1987). Therefore natural habitats closer to crops provide nesting places and a variety of feeding resources to arthropods, such as nectar, pollen and alternative preys that may enhance the abundance of natural enemies, as well as, their longevity and fecundity (Gurr *et al.* 2003b, Tylianakis *et* *al.* 2004, Drapela *et al.* 2008, Lee and Heimpel 2008, Pluess *et al.* 2010, Rusch *et al.* 2013a). However, resources provided by plants in natural habitats may also benefit herbivores in crops (Lavandero *et al.* 2006b), thus increased plant diversity *per se* may not result in a better pest suppression (Fiedler *et al.* 2008, Isaacs *et al.* 2009).

Despite the well known positive effect of plant diversity and landscape complexity on pest's natural enemies, the mechanistic link between biodiversity and provision of ecosystem services is still poorly understood (Shackelford *et al.* 2013). Most studies have been evaluated the impact of biodiversity on pest control using the abundance or richness of a services's provider as a proxy for ecosystem service (Shackelford *et al.* 2013) and examples of direct measurements of pest control are scarce (Gardiner *et al.* 2009). In addition, empirical evidence fails to demonstrate that increasing richness or abundance of natural enemies always translates in increased crop yield (Chaplin-Kramer *et al.* 2011). Clearly, the idea that higher biodiversity of natural enemies improves crop productivity through top-down effects on crop plants warrants more research.

Gaps in research remain in regards to the role of native forest on pest control, since most studies include a diverse set of land-uses within the category of natural habitats, e.g. flower strips, hedgerows, fallows, grassland and forest (Thies *et al.* 2003, Schmidt and Tscharntke 2005). Thus, knowing the particular role of native forest is relevant in multifunctional agroecosystems, in which this habitat plays an important role in the provision of several ecosystem services, including the conservation of wildlife (Perfecto and Vandermeer 2008). In addition, research efforts in these topics are biased to arthropods in temperate zones, and little is known about their effect on both arthropods and weeds in more complex agroecosystems, such as tropical indigenous crop systems.

Here we addressed these issues by studying the relationships between cover of native forest in the landscape and diversity of plants and arthropods, as well as, their relationships with herbivory and production in traditional cornfields. Previous analysis demonstrated that the diversity and richness of plants and herbivores were not related to the cover of native forest around the crops but it had an effect on species composition (EMP, Unpublished data). Therefore, we classified plants in three categories: grasses, non-grass weeds and low-dominance native species. This classification allows us to re-evaluate the relationships between plant diversity and the amount of forest taking into account some plant characteristics that affect pest management. For instance, grasses were considered by separated because they may serve as alternative host of the whorl worms such as

Spodoptera frugiperda J. E. Smith the main pest on corn (Pashley 1988). Therefore, grasses may affect corn yield by enhancing or reducing the cornfield susceptibility to the attack of whorl worms (Barbosa *et al.* 2009). Similarly, non-grass weeds may affect the production of corn negatively by competing with the corn plants or by enhancing populations of herbivores (Ryan *et al.* 2010, Smith *et al.* 2010). However, weeds may affect corn yield positively by enhancing populations of natural enemies in the cornfields (Fiedler and Landis 2007, Lu *et al.* 2013).

We examined the following predictions about the impact of native forest on biodiversity, herbivory and crop yield. First, we expect a positive relationship between cover of native forest and cover/abundance and species richness of plants, herbivores and pest's natural enemies in the cornfields. Second, we expect a significant positive relationship between the cover and richness of grasses and the damage inflicted to corn plants by whorl worms. Third, we expected a positive relationship between plant richness and abundance/richness of natural enemies, and a negative relationship between natural enemies and herbivory in corn plants. Fourth, we expect higher forest cover around the crops to results in the less the damaged inflicted by herbivores to the crop and higher crop yield.

We tested these hypotheses by selecting twelve traditional cornfields in the Colombian Andes. The cornfields were located in a gradient of forest cover within a radius of 250 m around on them, which enabled us to assess changes in diversity related to this factor. We also evaluated the effects of other covariates such as soil organic matter, field former land-use, altitude and perimeter-to-area-ratio of each cornfield. In such system we addressed the following questions: *i)* how do species richness and cover/abundance of weeds, grasses, native herbs, herbivores and natural enemies change in relation to percent forest cover around the crop? *ii)* How is the relationship between the crop infestation level by whorl worms and the richness or coverage of grasses and other weeds in cornfields? *iii)* How is the relationship between plant richness and the abundance and richness of herbivores, predators and parasitoids? And *iv)* to what extent are herbivory and crop yield affected by forest cover and the biodiversity associated with corn crops?

Materials and Methods

Descriptions of study area, as well as, environmental descriptors were described in the previous chapter.

Arthropod sampling. We sampled flying and leaf-dwelling arthropods on September and December 2011. Samples were taken by five sweep-nets that captured arthropods in the center of each cornfield. Arthropods were preserved in 70% alcohol for further identification to family level and morpho-species of herbivores and predators. We classified arthropods into five trophic groups (predators, parasitoids, herbivores, pollinators, nectarivores and saprophagous), according to reports in literature for families or genera (Kaston 1978a, Triplehorn and Johnson 2005, Fernández and Sharkey 2006a, Dippenaar-Schoeman and Jocqué 2007a). In order to get an accurate assessment of herbivore's effect on foliar herbivory, herbivores were classified in sap-feeders and leaf-chewers depending whether they had exogenous or endogenous feeding. For herbivores and predators we choose the abundance and the total number of morpho species as indicators of their diversity in cornfields, whereas for parasitoids we used abundance and the total number of families.

Weed sampling. We sampled plants on December 2011, four months after the corn sowing date. We randomly selected five rows in the center of each cornfield. On each, we used equidistant sampling stations along a 20 meter-long transect, thus totalizing 25 sampling stations per corn field. Each station was sampled by using a plastic quadrat (50 x 50 cm) divided in 100 subquadrats. We recorded the presence of all plant species in each station and counted the number of subquadrats occupied by each species as a measure of cover.

A measure of dominance of each specie per cornfield was estimated as the sum of their relative values of frequency and coverage. Relative frequency was estimated as the proportion of quadrats in which the specie was present in each cornfield, whereas the relative coverage was the sum of the coverage of each specie in all quadrants divided by the sum of the values of coverage for all species in each cornfield.

Due to the amount of forest around each corn influenced changes in plant species compositions in the studied cornfields (EMP Unpublished data), we classify plants in categories relevant to pest management: grasses, weeds and low-dominance species. Weeds included species with weed habit e.g. high values of dominance, as well as species reported as weeds in Colombia (Fuentes and Romero 1991). The reasons to separate grasses were given in the introduction, and as the dominant species may have a higher importance in ecological processes in cornfields than the occasional ones we decided to analyze them separately.

Foliar herbivory. We evaluated leaf damage on October 18 -24 (7-8 weeks after corn emergence), 2011 and January 2 – 5 2012 (4 month after corn emergence). A total of 30 corn plants per cornfield were selected randomly to evaluate herbivory using a weighted method to asses herbivory (Dirzo and Domínguez 1995b): each leaf of the plant is scored on a scale from 0 to 5, with 0 being a leaf with no damage, 1 a leaf with 1 and 6% of foliar consumption, 2 a leaf with a damage between 6% and 12%, 3 a leaf with a damage between 12% and 25%, 4 a leaf with a damage between 25% and 50% and 5 a leaf with more than 50% of foliar area consumption by herbivores. For each corn field we pooled the total number of leaves considering all plants and calculated the Herbivory index according to the following equation:

$$IH = \frac{\sum n_i \times i}{N}$$

In this equation n_i is the number of leaves in each category *i* multiplied by the category's value (0-5). N is the total number of observations.

Infestation of cornfields by whorl worms. On October 18-24th, 2012 (7-8 weeks after corn emergence), we evaluated the incidence of the major pest in corn crops (*S. frugiperda*) and other whorl worms in corn plants (e.g. *Copitarsia decolora* Guenée). We choose 100 corn plants randomly selected in each crop. Corn plants whorls were visually inspected looking for larvae or evidence of damage by whorl worms. We registered the proportion of plants with damage by whorl worms in each cornfield.

Crop yield. We randomly selected 10 plants per cornfield to evaluate production. All plants were harvested on January 18-30 2012 (5-6 months after sown). We separated vegetative structures from ears, and all materials were dried in an air flow stove (60°C) over the course of a week until constant weight. We registered the weight of healthy grain per plant and calculated the average of healthy grain per plant for each corn field for data analysis. We report mean values per plant as a measure of crop yield as a way to standardize for differences in among fields, such as field size and other physical properties.

Data analysis

Species richness. Sampling completeness was calculated in order to evaluate the adequacy of sampling effort. We developed species accumulation curves based on species presence-absence matrices by using the Incidence-based Coverage Estimator (ICE). These analyses were performed with the software Estimates, Version 8.2.0 (Colwell 2009) with 500 randomizations. The degree of saturation was indicated by the percentage of observed morpho-species relative to the estimated species richness. For plant sampling this value was 83% for pooled data. For arthropods completeness was 70%.

To evaluate the effect of the amount of native forest around the cornfields on plant and arthropod richness and foliar herbivory, whorl worm infestation level and corn yield crop, we used generalized linear models. Given the natural variation between fields, we used former land-use of each cornfield, altitude and field perimeter-area ratio in the models as a covariates. We also included in the model interactions between these factors and we scaled all predictor variables by mean and standard deviation.

We used Poisson log-link Regression to analyze discrete variables such as species richness. For continuous data, like crop yield and herbivory index, we used Ordinary Least Square Regression (OLS). For proportional data (whorl worm infestation level) we used logistic regression. In all cases we used stepwise forward simplification for model specification in order to comply with the principle of parsimony (Crawley 2003). To control for possible multicollinearity among predictors we calculated the Condition Number and the Variance Inflation Factor for OLS and Poisson Regression (Chen *et al.* 2003). We checked all model assumptions and all analyses were conducted using R software (R_Development_Core_Team 2008).

We used structural equation modeling (SEM) to examine the direct and indirect relationships among the availability of native forest, perimeter-to-area ratio, plant and arthropod diversity, herbivory and yield (Path Analysis). SEM analysis was based on a conceptual model built under the following premises: *i)* native forest may enhance arthropod diversity in crops because they may develop larger populations in permanent habitats and then spill over onto crops (Klein *et al.* 2006, Rand *et al.* 2006, Tscharntke *et al.* 2012); *ii)* plant diversity within the cornfields may enhance crop yield through a positive effect on natural enemies which benefit from extra-resources (food and shelter) that non-crop plants provide to them (Gurr *et al.* 2003b, Isaacs *et al.* 2009, Landis *et al.* 2012b) and; *iii)* higher herbivore abundance and richness may lead to higher herbivory and lower crop yield, due to the negative effects of herbivory on plant performance (Agrawal 1998). Former models also include control variables, such as the altitude, the percentage of soil organic matter and the percentage of soil organic carbon.

We fitted a theoretical model using the function SEM in R (R Core Team 2012) package lavaan (Rosseel 2012) and evaluated the adequacy of selected models by testing if there were no significant differences (P>0.05) between the likelihood of the model and data, via chi-square tests (Grace 2006). We also evaluated the explanatory power of competing models using the Akaike Criterion (AIC) (Burnham and Anderson 2004) by ranking candidate models according to ΔAIC (difference between model's AIC and min AIC). Lower ΔAIC indicates higher support for a given model.

Results

We registered a total of 198 plant species from 29 orders and 53 families in the corn fields. Most of them (N= 122) were low-dominance species (61.6%) with low relative frequency and coverage, followed by 45 species of weeds (22.7%) and 29 species of grasses (14.6%). The dominant weeds, plants with the highest values of frequency and coverage in the whole area, were *Pteridium aquilinum, Drymaria cordata*, *Cyperus* sp., and *Hedychium coronarium*. Grasses were dominated by *Brachyaria* sp (Appendix 3-1).

In regards to arthropods, we captured a total of 9043 individuals from eight orders and 116 families. Most of them were herbivores (66.1%), followed by predators (17.4%) and parasitoids (14.2%). Herbivores and predators were the most diverse groups with 254 and 152 morpho-species, respectively. The predominant feeding guild among herbivores was sap-feeders (63.0%), followed by leaf- chewers (30.3%) and finally, concealed feeders (6.7%) (Appendix 5-2).

Relationships between forest cover and plant richness and cover.

Plant richness did not correlate to changes in forest cover around on cornfields, regardless the group considered (Appendix 5-3). However, the coverage of weeds and low-dominance herbs, but not grasses, was higher in cornfields with higher proportion of forest around on them (Fig.5-1 a,c & e). Instead, different previous-land uses of cornfields were associated with changes on richness and coverage of grasses and low-dominance herbs, but not weeds (Fig. 5-2).

Other environmental factors, such as soil organic matter had positive relationships with the cover of grasses and weeds but no effect on low-dominance herbs (Fig 5-1 b, d & f). Soil organic matter was also positively related to the richness of weeds (Appendix 5-3). The perimeter-to-area ratio of each cornfield was related to higher cover of weed and grasses, but richness of species and cover of low-dominance weeds did not respond to changes in this factor (Appendix 5-3).

Responses of plants to changes in altitude were highly variable, having negative relationships with the coverage of grasses, but positive relationships with the coverage of weeds and the richness of low-dominance herbs (Appendix 5-3).

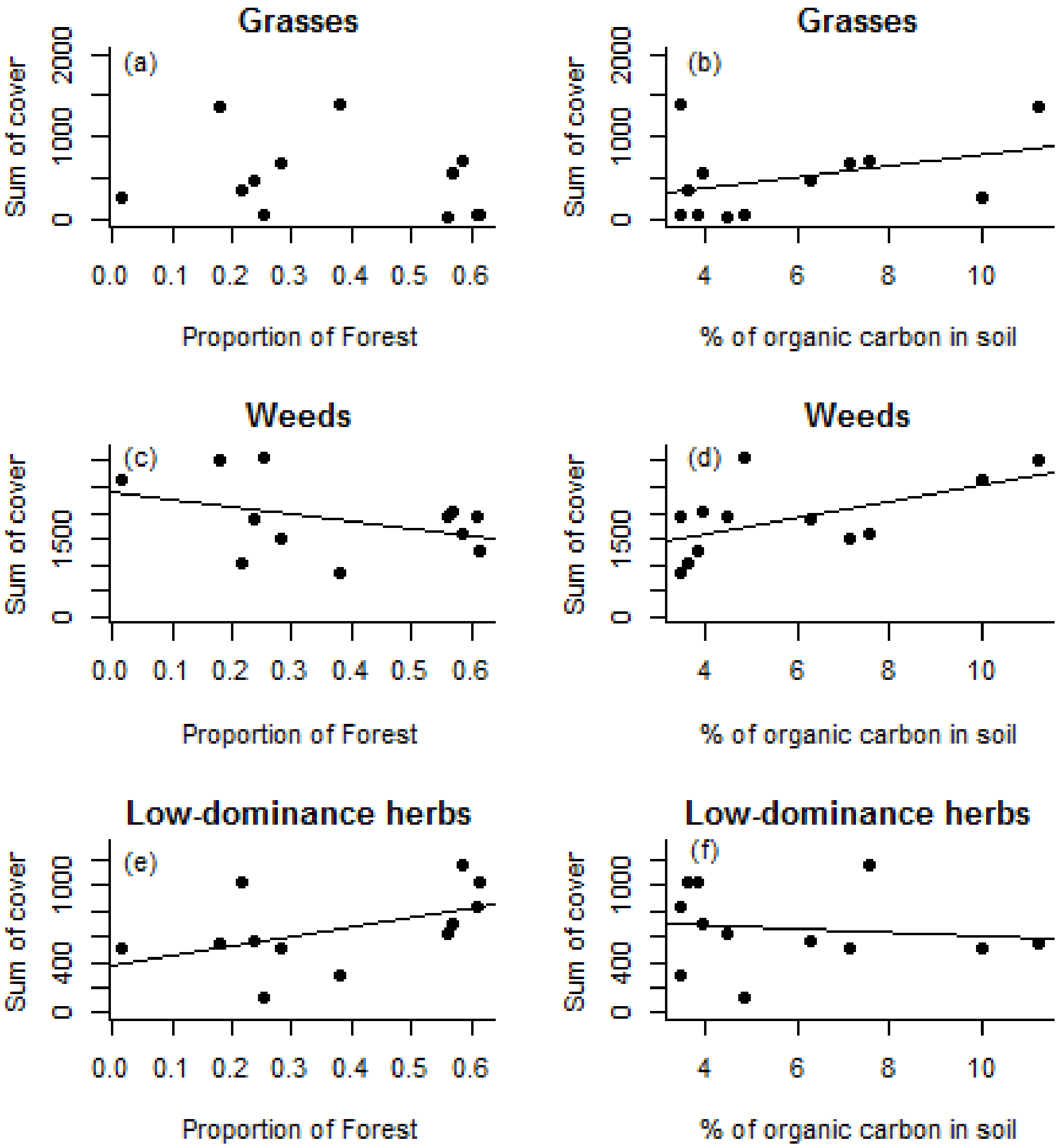

Figure 5-1. Coverage of grasses (a &b), weeds (c & d) and low-dominance herbs (e&f) measured on traditional cornfields in the Colombian Andes in relation to the proportion of forest in a radius of 250m around each crop (a,c & e) and the percentage of organic carbon in soils (b, d & f). Lines indicate predicted values of regression models, and it only were plotted when the relationships were significant at a 95% confidence level.

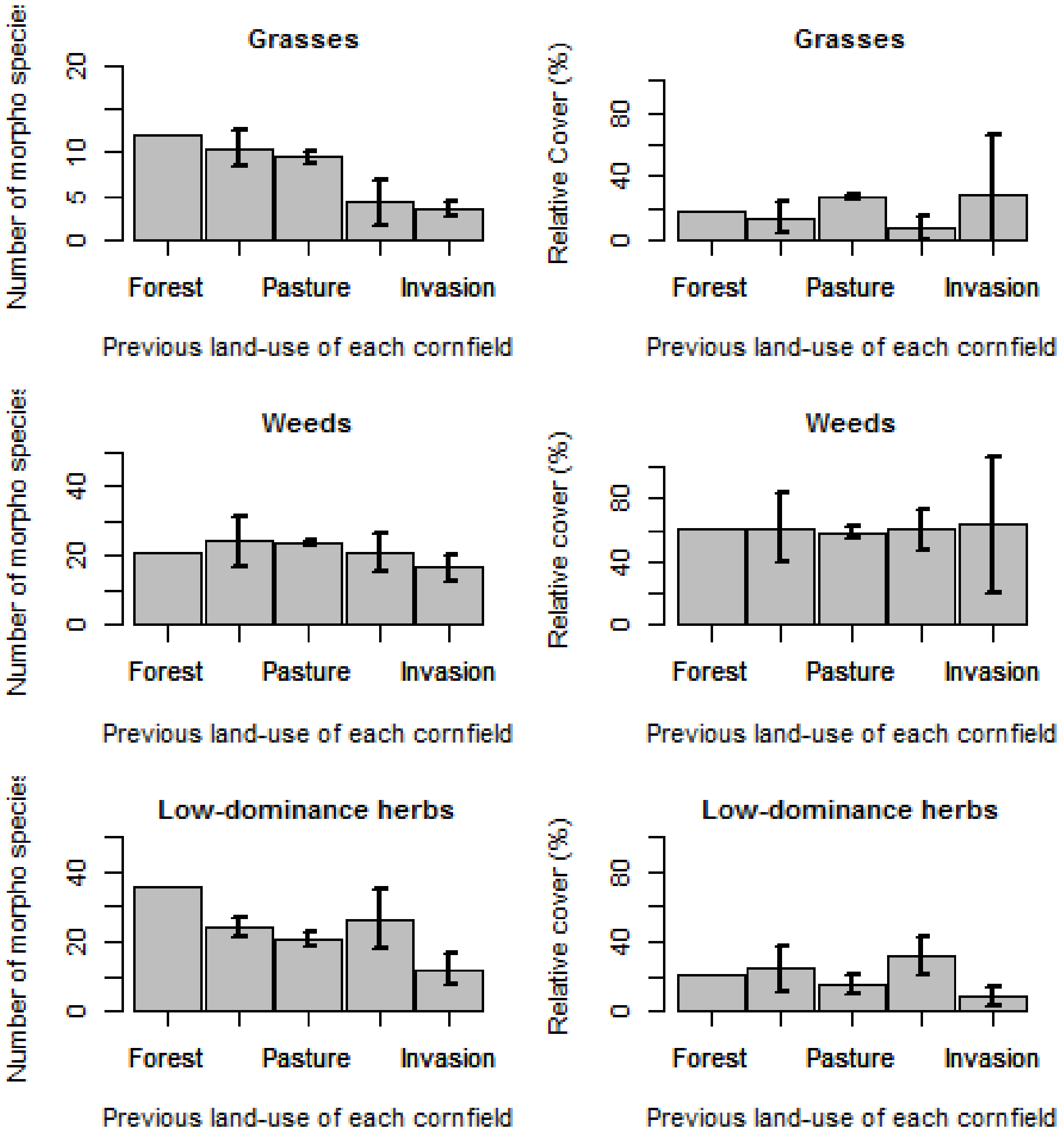

Figure 5-2. Mean number of morpho-species (left side) and mean values of relative coverage (right side) of weeds, grasses and low-dominance herbs (left side) collected in tradition cornfields in the Colombian Andes, in relation to the previous use of the crop fields: one field previously covered by forest; two fields planted with other crops; two fields covered by pasture; five fields in fallow and two fields covered by invasive herbs.

Relationships between forest cover and arthropod richness and abundance. The richness of leaf-chewers herbivores was positively correlated with the percentage of forest cover (Pearson's r = 0.58, p = 0.0463), but the rest of arthropod trophic groups did not respond to changes in forest cover around the crops, or to other environmental predictors (Appendix 5-4). Both altitude and forest cover within a radius of 250m around each cornfield had a negative relationship with the abundance of herbivores and parasitoids (Fig. 5-3 a,b & e,f), but predators did not respond to changes in these factors (Fig. 5-3c & d, Appendix 5-4).

The richness of plants was positively related to the richness of herbivores and predators, however these relationships varied among groups (Fig. 5-4). Only weed richness had a positive relationship with herbivore richness (Pearson's r = 0.86, p = 0.0003, Fig. 5-4b), whereas low-dominance plants were positively related to richness of predator (Pearson's r = 0.69, p=0.0124, Fig. 5-4c). Parasitoid family richness had lower variability among the cornfields and they did not respond to changes in plant richness (Fig. 5-4g-i, Appendix 5-4).

Grass richness was positively correlated to the abundance of herbivores and natural enemies (Fig 5-5a, d & g). Weed richness had a positive relationship with the abundance of parasitoids and herbivores (Fig. 5-5 b&h), but it was unrelated to changes on predator abundance (Fig. 5-5e). Overall, weed richness had a negative relationship with the abundance of herbivores, regardless the trophic group considered (Fig. 5-5b, Appendix 5-4). The richness of low-dominance plants had a positive relationship with the abundance of herbivores, but predators and parasitoids did not respond to changes in this variable (Fig. 5-5c, f & i).

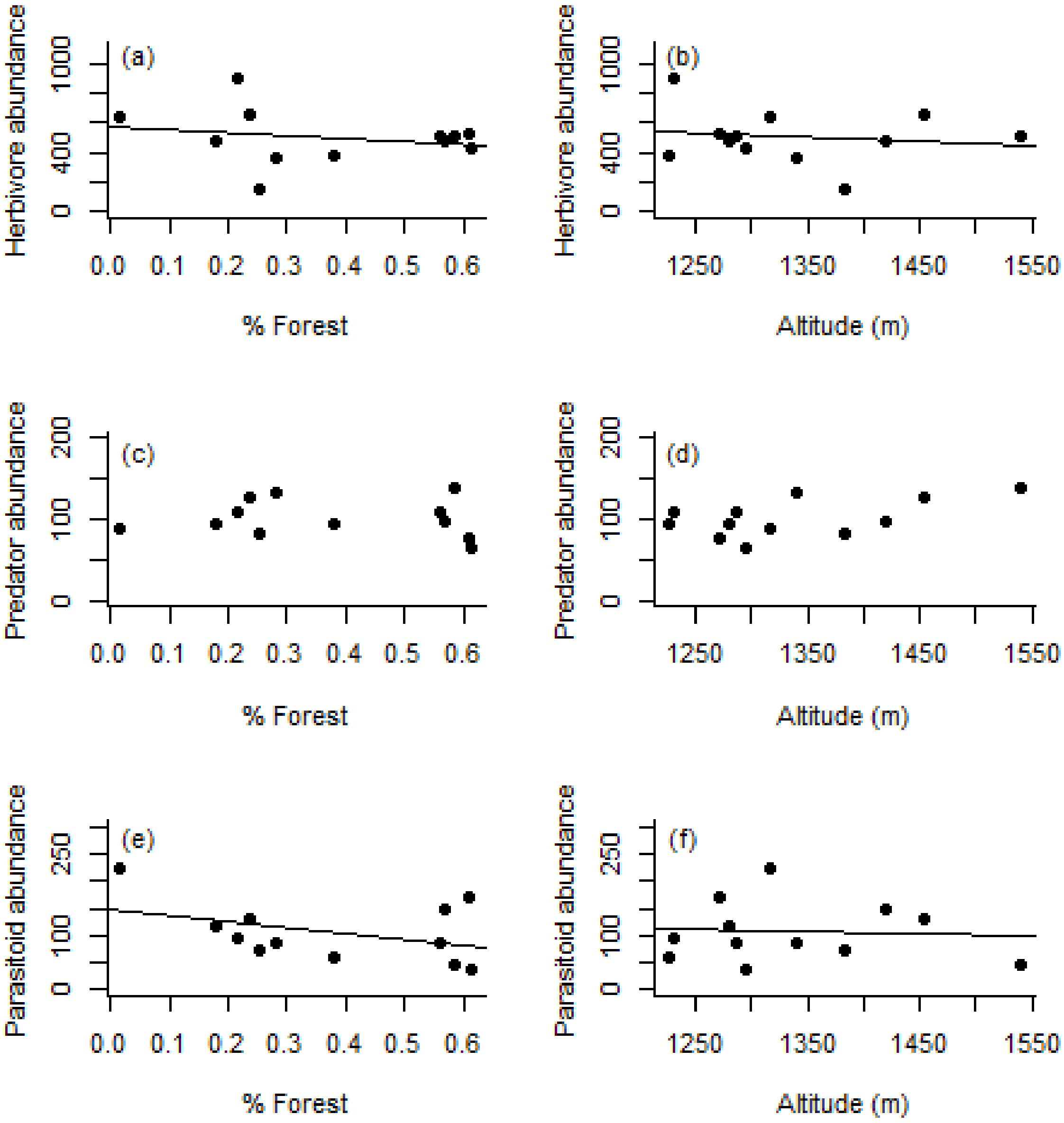

Figure 5-3. Abundance of herbivores (a & b), predators (c & d) and parasitoids (e & f) collected on traditional cornfields in the Colombian Andes in relation to the percentage of forest in a radius of 250m around each crop (a, c & e) and the altitude at the site of each cornfield (b, d & f). Lines indicate predicted values of regression models, and it only were plotted when the relationships were significant at a 95% confidence level.

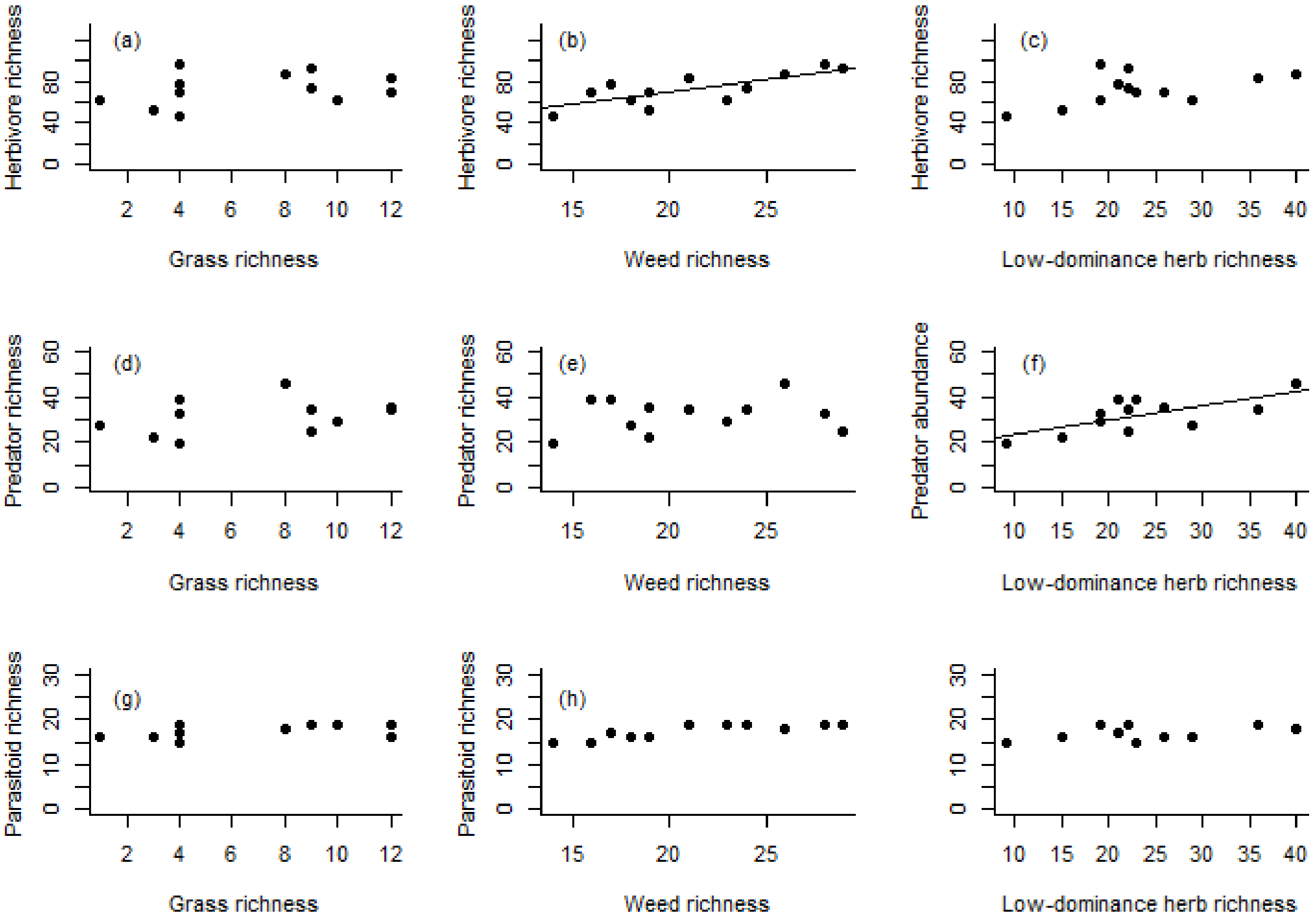

Figure 5-4. Morpho-species richness of herbivores (a - c), predators (d - f), and family richness of parasitoids (g - i) collected in traditional cornfields in the Colombian Andes in relation to the grass richness (a, d & g), weed richness (b, e & h), and low-dominance herb richness (c, f & i) registered in each cornfield. Lines indicate predicted values of regression models, and it only were plotted when the relationships were significant at a 95% confidence level.

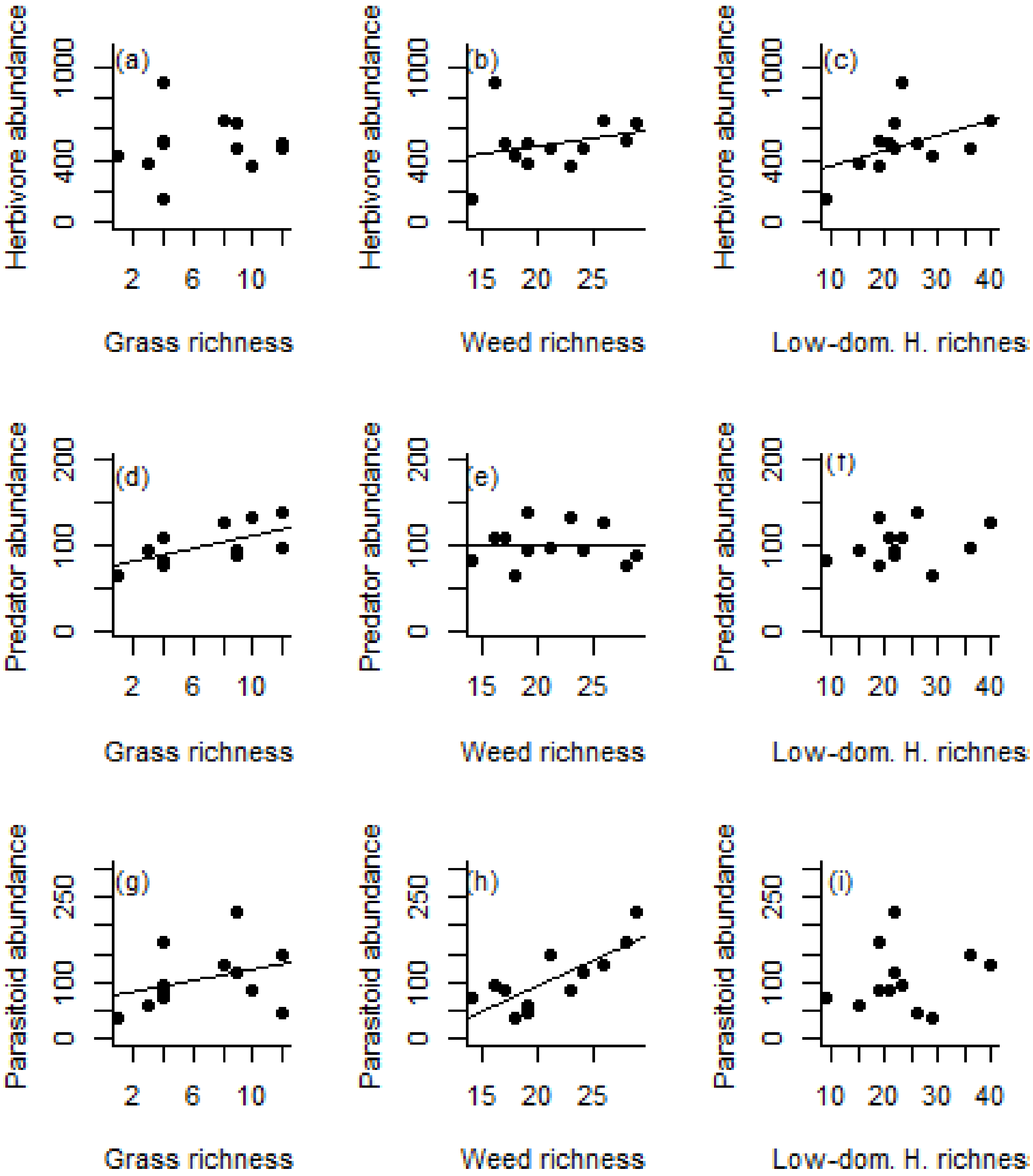

Figure 5-5. Abundance of herbivores (a - c), predators (d - f), and parasitoids (g - i) collected in traditional cornfields in the Colombian Andes in relation to the grass richness (a, d & g), weed richness (b, e & h), and low-dominance herb richness (c, f & i) registered in each cornfield. Lines indicate predicted values of regression models, and it only were plotted when a significant relationship between variables was found at a 95% confidence level.

Crop damage and yield. Field perimeter-to-area ratio of each field was positively correlated with the herbivory index in corn plants (Fig. 5-6a), the richness of leaf-chewer herbivores (Fig. 5-6b) and abundance of predators (Fig. 5-6d). Weed cover was positively correlated with foliar herbivory, but this relationship was only marginally significant (Fig. 5-6c, Appendix 5-4).

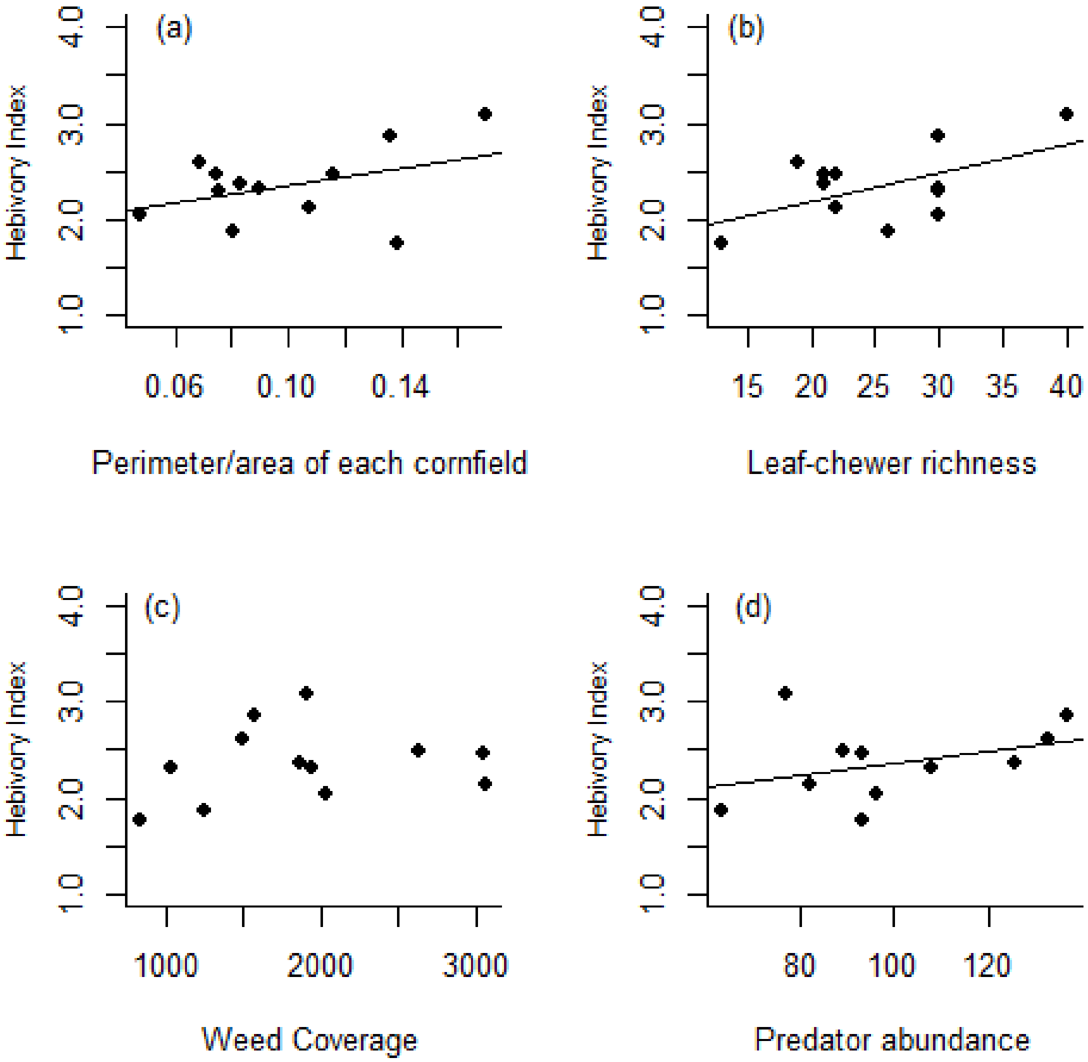

Figure 5-6. Herbivory Index measured in corn leaves in traditional cornfields in the Colombian Andes, in relation to the perimeter-to-area ratio of each field (a), the richness of leaf-chewer herbivores (b), the coverage of weeds (c), and the abundance of predators (d). Lines indicate model prediction values.

The richness of leaf-chewers herbivores was positively related to damage by whorl worms (Fig. 5-7a), whereas the richness of grasses had a negative relationship with this damage (Fig. 5-7b, Appendix 5-5). Neither the proportion of forest in a radius of 250m around the crop nor additional environmental predictors had a significant relationship with the proportion of corn plants affected by whorl worms. Finally, foliar herbivory had a negative relationship with the production of healthy grain in corn plants (R^2= 0.30, $F_{(1,10)}$= 5.78, p= 0.0369, Fig. 5-8).

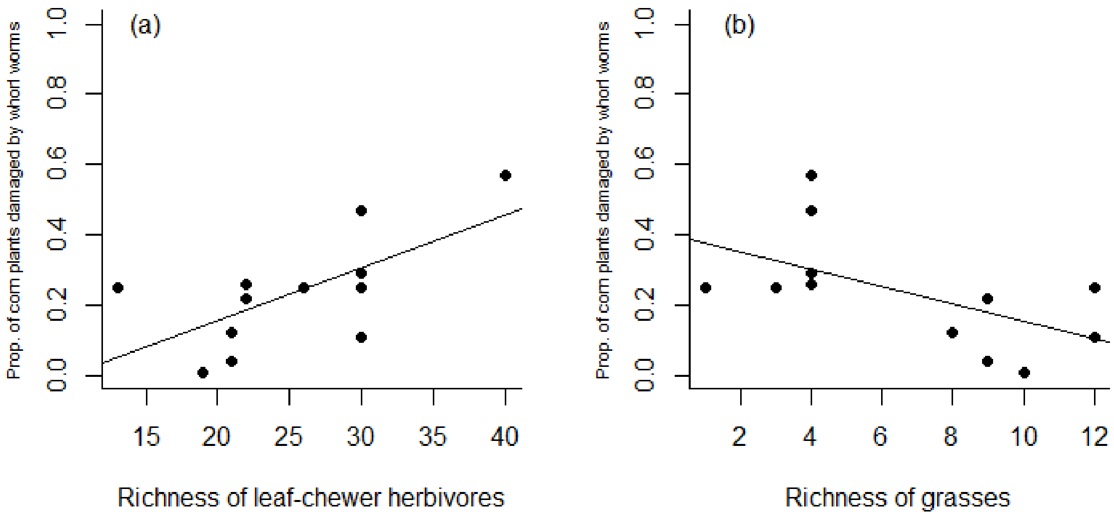

Figure 5-7. Proportion of corn plants damaged by whorl worms in traditional cornfields in the Colombian Andes, in relation to the richness of leaf-chewer herbivores (a) and the richness of grasses (b). Lines indicate model prediction values.

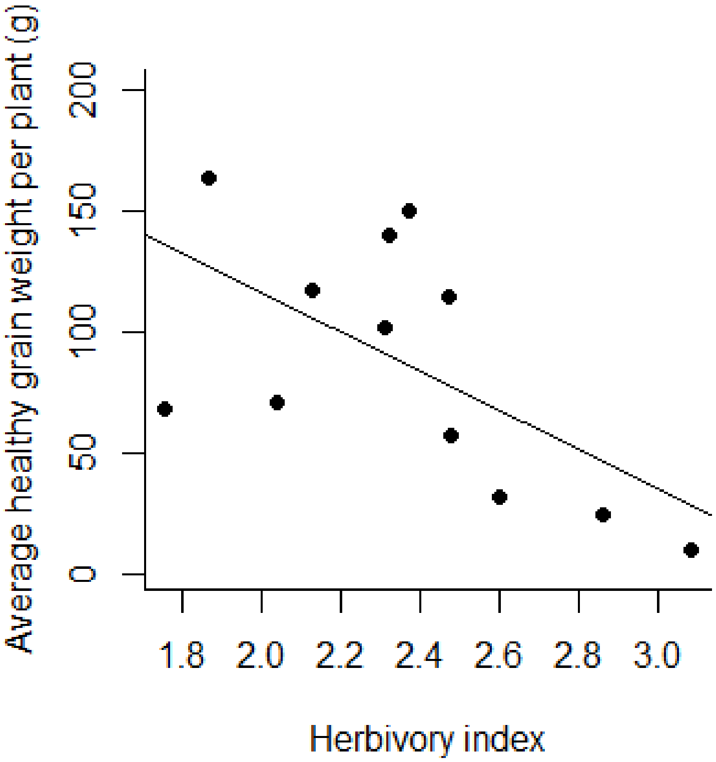

Figure 5-8. Average weight of healthy grain produced per plant in relation to foliar herbivory measured in traditional cornfields in the Colombian Andes. Line indicates model prediction values

The path analysis evaluating relationships between forest cover, weed and arthropod diversity, herbivory and corn yield fitted the data adequately (CFI= 0.85, RMSEA=0.25 p=0.11, and Chi-square= 12.01, p=0.098). This analysis showed that cornfields with a more rich assemblage of leaf-chewer herbivores had higher foliar herbivory on corn plants, and this damage reduced corn yield. Weed richness did not affect production directly, but indirectly enhanced corn yield by increasing the abundance of natural enemies -particularly of parasitoids-, which in turn was negatively related to the richness of leaf-chewing herbivores (Fig. 5-9).

The richness of leaf-chewer herbivores was higher in cornfields with higher proportion of forest around on them. Thus, forest increased foliar herbivory indirectly, which in turn reduced the production per plant. Cornfields with higher edge effect due to high values of perimeter-to-area ratio tended to have higher herbivory, but this variable had no significant impact on any of the study factors (Fig. 5-9).

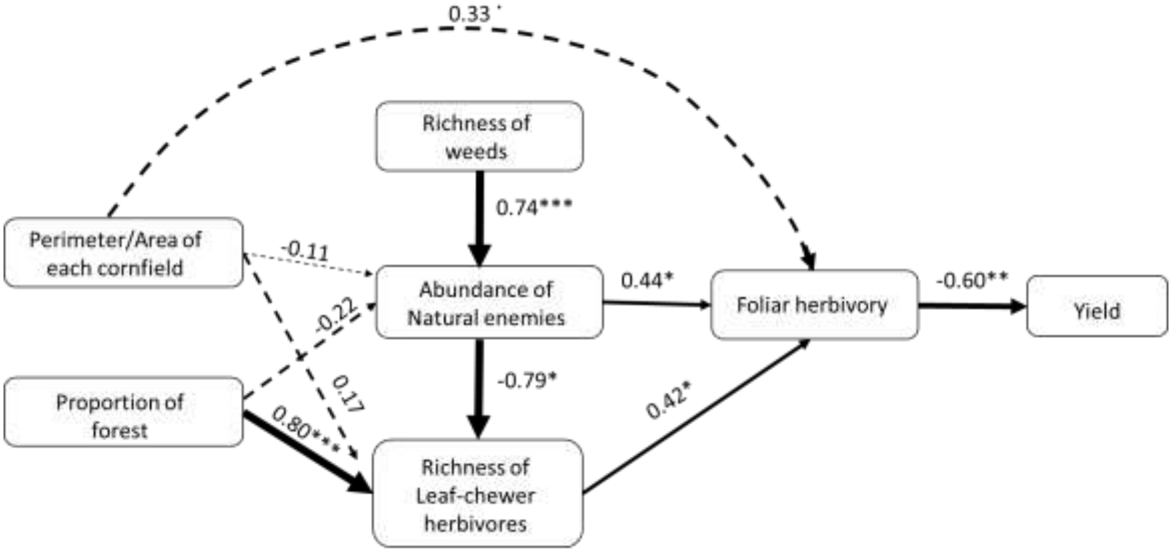

*Figure 5-9. Path diagram for direct and indirect relationships among the proportion of native forest in a radius of 250m around each cornfield and the perimeter-to-area ratio of each crop field, the richness of weeds, the abundance of natural enemies, the richness of leaf-chewing herbivores, foliar herbivory and corn yield. Solid lines indicate significant effects and dashed lines indicate a non-significant effects. .Width of each line is proportional to the strength of the relationship. ·P<0.1, *P <0.05, **P <0.01, ***P <0.001.*

Discussion

Contrary to previous findings suggesting that natural enemies are more diverse and abundant in landscapes containing large amounts of natural or semi-natural habitats (Öberg 2007, Schmidt *et al.* 2007, Oberg *et al.* 2008, Gardiner *et al.* 2009, Diekötter *et al.* 2010, Ekroos *et al.* 2010, Pluess *et al.* 2010, Chaplin-Kramer *et al.* 2011, Woltz *et al.* 2012) , a larger amount of forest around the crop fields did not enhance the abundance or richness of predators and parasitoids in cornfields. Even more, the abundance of parasitoids was lower in cornfields with higher proportion of forest around on them. In addition, forest cover indirectly enhanced foliar herbivory in corn plants through its positive relationships with the richness of leaf-chewer herbivores.

Antagonistic interactions such as intra-guild predation has been suggested as the main mechanism explaining why pest control is constrained in complex landscapes. Thus, increasing the proportion of intraguild predator species diminish herbivore suppression (Finke and Denno 2005). For instance, when crops are embedded in complex landscapes, e.g. with larger amounts of natural habitats, hyper-parasitism rates may be higher (Thies *et al.* 2005), and the presence of insectivorous birds may reduce pest control performed by insects (Martin *et al.* 2013). Antagonistic interactions between predator are likely to operate in the studied cornfields, because they had a diverse assemblage of generalist predators, in which intraguild predation have been reported previously as a common phenomenon (Rickers *et al.* 2006).

In regard to herbivores, their responses to changes in forest cover differed between trophic groups. Forest cover had positive relationships with the richness of leaf-chewer herbivores, but was negatively related to the abundance of sap-feeders. These results support evidence that habitat loss does not affect all species equally (Butsic *et al.* 2012, Tscharntke *et al.* 2012). Thus, responses of organisms to landscape complexity vary among taxa and will depend on habitat suitability to each species, as well as, on species characteristics such as feeding habit, body size, dispersion capacity and population size (Tscharntke *et al.* 2005a, Tscharntke *et al.* 2005b, Fahrig *et al.* 2011a). Then a functional characterization of diversity is needed to understand how habitat loss affects pest control and other ecosystem services in agroecoystems.

Our results contrast with previous works suggesting that parasitoids assemblages are more diverse and abundant in more complex landscapes (Haenke *et al.* 2009, Jonsson *et al.* 2010, Letourneau *et al.* 2012b). Given that herbivore’s feeding niche has a major influence on the number of primary parasitoids, as well as on hyperparasitoids (Hawkins 1994), it is possible that the observed negative relationships between forest cover and herbivore abundance had translated into a reduced abundance of parasitoids in cornfields with larger amounts of forest around of them. In addition, the distribution of parasitoids is also related to the availability of resources provided by plants in the agricultural landscape. For instance, nectar and pollen may enhance the longevity and fecundity of parasitoids (Tylianakis *et al.* 2004, Berndt and Wratten 2005, Lee and Heimpel 2008) and plants host herbivores that could serve as alternative host for parasitoids (Barberi *et al.* 2010). Plant diversity was high in all cornfields regardless the cover of forest around them, floral resources and alternative host were available in more transformed areas, leading to more abundant assemblages of parasitoids in cornfields isolated from forest. Therefore, plant diversity and host distribution directly influence the abundance of parasitoids in cornfields, whereas the cover of forest in the landscape may have an indirect influence on parasitoids by reducing the availability of herbivores in adjacent cornfields. However, a more detailed analysis of parasitoid species composition and behavioral ecology is needed to get insight into understanding how species perceive their environment, as well as in evaluating habitat suitability from the insect's perspective (Fahrig *et al.* 2011a).

Given that the richness of plants did not respond to changes in forest cover, our data do not support the expectation that landscape complexity enhanced the diversity of arable weeds (Roschewitz *et al.* 2005). However weed cover and low-dominance herbs, but not grasses were positively correlated to forest cover. In addition, weed and grass coverage was higher in smaller-size area cornfields, with high perimeter-to-area ratio and higher content of soil organic matter. The previous land-use of the cornfields was the most important factor influencing changes in the richness of low-dominance plants and grasses, as well as, in the coverage of all groups of plants. Overall species richness of plants was lower in cornfields previously covered by pastures, as well as, in cornfields previously covered by invasive plants. Similarly, cornfields previously covered by fallows had lower coverage of grasses and weeds, but higher coverage of low-dominance weeds. These results support the idea that weed communities are mainly affected by local conditions and crop abiotic factors, such soil properties, preceding crop type, fertilization, tillage and land drainage (Navas 2012). In addition, plant diversity in each field may reflect the composition and size of the seed bank, which in turn is mainly affected by field management (Franke *et al.* 2009). So further research should evaluate the expression of seed bank, as well as, the responses of arable weeds to management practices.

The diversity of plants in the crop fields influenced the richness and abundance of overall arthropods collected in the cornfields. Weed richness enhanced pest control in traditional cornfields through their positive relationship with the abundance of natural enemies, particularly with parasitoid abundance, which in turn were related to lower richness of leaf-chewer herbivores. In addition, the richness of grasses were related to lower incidence of damage inflicted by whorl worms in cornfields. These results are consistent with the 'enemies hypothesis' which predicts that abundance of predator and parasitoids will be augmented in species-rich plant assemblages and thereby control herbivores more effectively (Risch 1987). Therefore, resources provided by weeds in traditional cornfields enhance pest control probably by increasing the fecundity and longevity of natural enemies, which has been previously documented (Tylianakis *et al.* 2004, Lee and Heimpel 2008). A positive relationship between the richness of low-dominance herbs and the richness of predators also support this hypothesis and agree with previous work suggesting that plant diversity within crop reinforces the richness of natural enemies (Altieri and Letourneau 1982, Gurr *et al.* 2003b, Isaacs *et al.* 2009, Barberi *et al.* 2010, Letourneau *et al.* 2011).

The fact that grass richness had a negative relationship with the incidence of damage of whorl worms (e. g. *S. frugiperda* and *C. decolora*) in the studied cornfields, suggests that grass diversity may decrease crop's susceptibility to the attack of these herbivores. This result is consistent with the idea of associational resistance, which propose that specific plant associations may decrease the likelihood of detection by, and/or vulnerability of focal plants to herbivores (Barbosa *et al.* 2009). Thus, further research in pest managemet strategies of whorl worms based on plant diversity and insect's behavioral ecology (e.g. trap crops and repellent plants) should focus on grass species.

On the other hand, the richness of weeds and low-dominance herbs had a positive relationship with the richness of sap-feeder herbivores, but their abundance was negatively related to it. Unlike the richness of grasses was positively related to the abundances of both, leaf-chewers and sap-feeders herbivores. These results highlight the positive role of arable weeds in pest control in traditional cornfields, and suggest complex mechanism involving associational resistance, enhancing natural enemy's populations and possibly, more attractive plants to herbivores, e.g. grasses (Poveda *et al.* 2008, Barbosa *et al.* 2009, Barberi *et al.* 2010) In addition, the richness of plants did not show a negative relationship with crop production. Thus the specific farmer's knowledge about the right time of weeding in cornfields enhanced the benefits that arable weeds provided to corn crops.

We observed that foliar herbivory in corn decreased the production of healthy grain per plant and that richness of leaf-chewing herbivores was the best predictor for this foliar herbivory. As foliar herbivory measured the amount of foliar area consumed by herbivores, it is reasonable to argue that changes in this variable were mainly explained by the richness of leaf-chewer herbivores and not by the species richness of sap-feeders herbivores. This result agree with the expectation that herbivory may reduce plant performance (Agrawal 1998) leading to a reduction in crop yield.

The path analysis confirmed the positive but indirect effect of plant diversity on crop production, by enhancing the abundance of natural enemies and pest control in cornfields, as well as, the negative indirect effect of forest on corn yield by enhancing the richness of leaf-chewer herbivores and herbivory in the studied crops.

This apparently “dis-services” of forest in pest control need to be considered with caution. For instance, soil organic matter is higher in cornfields closer to forest, and such conditions is related to higher richness and cover of arable weeds, which in turn enhanced pest control. Thus, the assessment of the importance of native forest for agriculture should take into account multiple ecosystem services in the same area (Raudsepp-Hearne *et al.* 2010), as well as, the cultural and socio-economics processes that affect their management (Swinton *et al.* 2007). Such methodological approach would give more insights into understand the components and processes that make traditional agriculture multifunctional and more sustainable (Altieri 2004, Gliessman 2007, Vandermeer 2011). Therefore, further research about the importance of forest in agriculture should consider their role in other ecosystem services, e.g. in water provision, preservation of soil nutrients and high content of soil organic matter, control erosion and flooding, provision wood and other non-timber-resources, as well as, in conservation of wildlife (Tilman *et al.* 2002, MEA 2005, Perfecto and Vandermeer 2008).

To sum up, the traditional cornfields studied are a good example of sustainable agriculture, given that production of corn is carried out with minimum external inputs and pest regulation is achieved by maintaining an outstanding diversity of plants inside the cornfields. Management of pest and weeds are based on local knowledge, by avoiding to sown corn during months with higher pest pressure and by controlling weeds in critical stages of the crop. This crop systems resembles natural ecosystems in different ways, such as high diversity, complex interactions between components, and minimum loss of nutrients. To improve crop yields in such system, more attention have to be paid to aspects such as field size and shape, in order to reduce edge effects and avoid higher press of herbivores on field margins.

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6. Limited effect of diurnal and nocturnal vertebrate predators on pest control in maize crops

Abstract

Vertebrate predators can reduce the pest population in agricultural crops and their effect can cascade down to plants, improving yield crops. Partitioning the global impact of vertebrate predators into diurnal and nocturnal species, and evaluating the influence of forest cover on their activity may improve our understanding of mechanisms underlying top-down controls in agro-ecosystems.

We conducted two predator-exclusion experiments to measure i) the differential impact of diurnal and nocturnal vertebrate predators in terms of herbivore damage and overall productivity in corn plants, and, ii) the effect of landscape structure on the relative importance of vertebrate predators on pest control in maize plants. Additionally, we estimated the rate of consumption of cobs by vertebrates and carried out a survey with maize producers to document local extinction or reduction of vertebrate predator species.

Both experiments involving predator-exclusion had the same results in which no significant difference was observed in herbivory or production between corn plants exposed to vertebrate predators and corn plants located inside enclosures. The average consumption of cobs by vertebrates was 5.72% ±. 4.19% with an extreme value of 45% observed in a cornfield with strong edge effect due to small size area. The perceptions of corn producers suggests that damage inflicted by vertebrate herbivores and particularly squirrels, has increased over the last 30 years. At the same time, producers reported that the potential predator vertebrates of these herbivores have been locally extinct or their abundance has been reduced.

A high diverse assemblage of pest’s natural enemies in complex agroecosystems may constraint pest control due to complex food webs, in which omnivory and intraguild predation are common. In such system, diurnal and nocturnal predators have an equally important role in pest control in cornfields, and an additive effect on pest-suppression in maize crops. Damage by granivorous vertebrates could be minimized by encouraging conservation of

carnivore taxa and by reducing edge effects through changes in the shape and size of the cornfields.

Keywords. De-faunation, Herbivory, Pest Control, Predator exclusion, Traditional crops, Vertebrate predators, *Zea mays* (L).

Introduction

Hairston *et al.* 1960) introduced the notion of predation or top-down control, as an essential force structuring natural communities. They stressed the importance of natural enemies in controlling herbivores as one mechanism to explain why the world is green. According to their hypothesis, the action of natural enemies keeps herbivore populations below the levels at which they would otherwise exhaust their food supply. Biological pest control in agricultural fields is based on such top-down forces. Most studies on biological control have focused on pest's arthropod natural enemies like predators and parasitoids, however, recently a growing number of studies have evaluated the role of vertebrates in pest control. For instance, predation on agricultural pests by insectivorous birds reduces plant damage and mortality (Van Bael *et al.* 2008, Philpott *et al.* 2009, Mantyla *et al.* 2011) and may reduce the frequency of required spraying and ultimately delaying the need for new pesticides (Federico *et al.* 2008, Kellermann *et al.* 2008, Johnson *et al.* 2010).

These positive effects of organisms in higher trophic levels (e.g. insectivorous bats and birds or predators and parasitoids) on plants through predation of herbivores, are known as trophic cascades, which are common in natural ecosystems (Schmitz *et al.* 2000) as well as in agricultural ones (Halaj and Wise 2001, Mantyla *et al.* 2011). Most evidence for trophic cascades comes from predation exclusion experiments in which plants benefits from natural enemies (Halaj and Wise 2001, Mantyla *et al.* 2011). For instance, numerous experiments on predation exclusion in agricultural crops have demonstrated that plants outside predator exclosures had less damage and lower pest infestation levels (Aflegrim 1989, Greenberg *et al.* 2000, Tremblay *et al.* 2001, Mols and Visser 2002, Hooks *et al.* 2003, Kellermann *et al.* 2008, Johnson *et al.* 2010, Xiao and Fadamiro 2010). In the majority of these studies the effects are attributed to birds, however, the enclosures used also restricted the entrance of both diurnal and nocturnal predators. Partitioning the effects of diurnal and nocturnal predator groups is essential for understanding the respective roles of vertebrates in agricultural pest control, especially because bats are important predators of agricultural pest (Cleveland *et al.* 2006, Federico *et al.* 2008, Williams-Guillen *et al.* 2008).

On the other hand, cultivated areas may attract granivorous vertebrate species that exploit temporal pulses of abundant resources in crops. For instance, in sorghum crops in Brazil the rate of grain consumption for granivorous birds was estimated in more than 30% (de Melo and Cheschini 2012), whereas, birds and small mammals were responsible for 9% of harvest losses in cornfields in Mexico (Romero-Balderas *et al.* 2006). Thus, evaluating the role of vertebrates in tropical agroecosystems should consider their relative contribution to pest control, as well as, their impact on crop yields through herbivory.

Finally, pest suppression in agricultural crops by vertebrates could diminish if habitat disturbance and fragmentation increases the mortality of bats (Kunz *et al.* 2011) and causes the disappearance of insectivorous birds (Sekercioglu *et al.* 2002). Predator-exclusion experiments and bird census in coffee agroecosystems suggest that habitat heterogeneity may allow primary predator to provide pest control broadly, despite localized farming intensity (Kellermann *et al.* 2008). Likewise, a forest matrix around sorghum crops had lower damage by granivorous birds, suggesting a positive effect of forest by providing enough resources for birds and by acting as barriers to “farm-land granivorous species” which prefer more open habitats (de Melo and Cheschini 2012). However, more research is needed to have more insights into understanding the impacts of agricultural intensification on ecosystem services and disservices (Zhang *et al.* 2007) provided by vertebrates in croplands.

To evaluate the contribution of vertebrates to pest control and herbivory in croplands we combine an experimental and observational approach with farmer’s perception surveys about vertebrates’ role in traditional cornfields in the Colombian Andes. The cornfields were located in a gradient of forest cover, which enable us to assess changes in insect foliar herbivory, vertebrate damage and corn production in relation to this factor. In this context we formulated the following questions: *i)* to what extent are herbivory and production of corn plants affected by the exclusion of diurnal and nocturnal vertebrate predators? *ii)* How to vary herbivory and production of corn plants excluded from predators in relation to changes in forest cover around each cornfield? *iii)* How much corn yield is affected by granivorous vertebrates? *iv)* What are farmer's perceptions about the changes in abundance of vertebrate predators and about their role as herbivorous in cornfields?

Firstly, we expect that excluding vertebrates predator from corn plants translates into higher populations of whorl worms (e.g. *S. frugiperda* and *C. decolora*), increasing foliar herbivory while reducing corn production in enclosed plants. Secondly, we expect a similar contribution of diurnal and nocturnal predators on pest control. Thirdly, we expect forest cover would have a positive relationship with the pest control performed by vertebrates, as well as lower damage of vertebrates as the cover of forest surrounding each cornfield increases.

This study contributes to understand the differential role of birds and bats in controlling pests in cornfields and also allows us to understand how habitat heterogeneity affects top-down controls in agro-landscapes. The results can be useful for designing pest control strategies based on habitat manipulation and conservative biological control.

Materials and methods

Study area. Fieldwork was carried out from August 2011 to February 2012 at the municipality of Topaipí, Cundinamarca; a rural area located on the west slope of the Central Cordillera in Colombian Andes (5 23.366N, 74 18.125W). In this region, we choose twelve traditional cornfields each of which is at least 230m from each other. All fields had small areas, which varied from 591 to 5112 m2. Cornfields were embedded in a landscape sector of 14 km^2 in an altitudinal gradient ranging from 1296 to 1550 m.

The landscape in this region is a mosaic of native forest and human land-uses such as cultivated fields, fallows and pastures; but forest still covers more than 50% of the municipality (EMP Unpublished data). Annual rainfall in the region is 2525.8 mm with peaks in April and September, whereas average temperature was 21.3°C ranged from 19.9 to 23.3 °C. Extensive grazing is the main source of farmers' livelihood, but they also grow marketable crops such as coffee and sugar cane. Subsistence crops included cassava, green banana, and corn, which are mainly grown on steep slopes close to remnants of native forest. However, some farmers also grow these crops in more transformed areas such as home gardens.

Forest cover and other environmental descriptors. We registered geographical coordinates, altitude and area for each cornfield by using a GPS. We mapped the land-use types within a radius of 250 m around each cornfield, through field visits and inspections of aerial photographs (GSD = 27.7 cm), and then we estimated the amount of area covered by each-land use type using Arcview 3.2 (ESRI 2009). We classified land-use types in the study area as native forest, secondary growth, hedges, pastures, transitional crops, perennial crops, home gardens and constructions.

We observed a gradient in forest cover from 0 to 62%. This variable was negatively related to cropped area (Pearson’s r = -0.80, p = 0.0017) and to habitat heterogeneity (r = -0.87, p = 0.0007), which was measured as the Shannon's Index for landscape data (Turner 1989).

Experimental design. We conducted two predator exclusion experiments in order to evaluate the ecological effect of vertebrate predators on herbivory and production in traditional maize crops. In the first experiment we compared the effect of diurnal and nocturnal exclusion of vertebrates on herbivory and production. In the second experiment we took into account the effect of landscape context on the result of predator exclusion treatment. In both experiments mesh exclosures permitted access to arthropods but prevented vertebrate (birds or bats) from gleaning them off of the plants.

Ecological effect of diurnal and nocturnal vertebrate predators on herbivory and production of corn plants. A randomized block design was used to evaluate differences in leaf and grain damage along with production between corn plants excluded from vertebrates and control plants totally exposed to vertebrates.

We chose one cornfield of 3036 m^2 in the study area (5°23'35, 1’’ N, 74°17'52,4" W, altitude: 1273m). In this field we selected eight blocks with four plants each one. Within each block, plants were randomly assigned to the treatments and control. The treatments consisted on plastic net enclosures that maintained corn plants inaccessible to vertebrates. In the first treatment, corn plants were excluded from nocturnal vertebrate predators (N = 8). In the second, corn plants were inaccessible to diurnal vertebrates, and in the last treatment, corn plants were totally inaccessible to vertebrate (N=8). Controls for these treatments consisted of uncovered corn plants, in which vertebrates had free access during the entire season (N = 8).

Exclosures were constructed with plastic nets 2.8m high with a mesh size of 2.5 x 3.0 cm. Four bamboo poles 3.4 m long, sunk 60 cm into the ground in the corner of one square of 80 x 80 cm were used to support the net. A field assistant, from September 8th, 2011 to December 28th, 2012 performed the opening and closing of the exclosures personally (at 6:00 am and 18:00 hours every day).

We evaluated leaf damage on October 20th 2011 and January 2th 2012 following Dirzo's methodology (Dirzo and Domínguez 1995a) According to this method, each leaf of the plant is scored on an herbivory scale from 0 to 5, with 0 being a leaf without herbivory and 5 a leaf with more than 50% of foliar area consumption by herbivores (Appendix S1). For each plant we estimated the Herbivory Index (IH) according to the following equation:

$$IH = \frac{\sum n_i * i}{N}$$

In this equation n_i indicates the number of leaves in each category multiplied by the score i (0-5), an N indicates the total number of leaves evaluated.

All plants were harvested on January 18th, 2012. We separated vegetative structures from cobs, and all material was dried in an air flow stove at 60 ˚C, over the course of a week until constant weight. Finally, we registered the weight of healthy grain per plant.

Effect of landscape on biological control of maize pest provided by vertebrate *predators.* We used a factorial design to evaluate the effect of both landscape and vertebrate exclusion on foliar herbivory, grain damage and production of corn plants. Based on forest cover we classified the twelve cornfields in two groups: those fields surrounded by less than

35% of forest were considered the group of “agricultural context”, whereas those surrounded by more than 35% of forest were considered in the group of “forest context”.

The exclusion experiment was set up in a 8m^2 plot located at the center of each field. In each plot three plants were randomly selected and covered with mesh exclosures, whereas controls were randomly selected between the closer corn plants around the treated one. The exclosures remained closed during the entire season, since September 8th 2011 up to harvest time in January 18th2012.

We compared leaf damage on October 20-24th 2011 and between January 2-8th, 2012 on maize plants inaccessible to vertebrate predators and controls. At the time of harvest we measured on each plant the healthy grain weight and the proportion of cobs with damage by herbivores.

Assessment of cobs damage by vertebrate herbivores. At each maize field we randomly chose 100 plants. On each plant we registered the proportion of cobs with evidence of damaged inflicted by vertebrate herbivores, which leaves a signal (scarf) easily recognizable by corn producers.

De-faunation surveys. Surveys were conducted on October 6th, 2012 in a meeting with 68 small landholders from the study area. Each participant had planted corn on his farm. Before the survey, a list of vertebrate species including mammal predators, as well as, herbivores present in the region was made according to information provided by Alberico *et al.* 2000). Slides of each species were shown to the landholders while we asked questions regarding the presence of each animal in the region and about its past (30 years ago) and present abundance. We also asked the participants about their perceptions of squirrel damage in maize crops; in particular, if they believed that the damaged has increased over the last three decades.

Data Analysis. We conducted a permutation test in order to compare the differences in herbivory and production on maize plants among inaccessible plant treatments and controls. We used a null scenario of non-differences with 1000 simulations. We calculated P-values that represent the probability that observed differences between control and treated plants came from the same distribution of a non-difference scenario. The same procedure was used to evaluate the effect of landscape complexity and vertebrate exclusion treatment on herbivory and production, but differences between treated plants and controls were evaluated separately for each landscape context.

Logistic regression model was used to analyze the effects of field traits (altitude, perimeter area ratio and cover of forest) on the proportion of cobs with damage by vertebrates. Outliers and influential points were identified graphically by plotting normalized residuals squared against leverage (Chen *et al.* 2003). Points with the largest leverage and the largest residual square were checked before to define the model. All statistical analyses were performed using the statistical program R, version 2.15 (R Development Core Team 2012).

Results

Ecological effect of vertebrates predators on herbivory and production*.* Low levels of foliar herbivory were measured in all treatments and control plants (Table 6-1), with an average score around two, which indicates that between 6% and 12% of foliar area of corn plants was removed by herbivores. Nocturnal, diurnal and total exclosures did not increase foliar damage in maize plants, given that observed differences between control and treated plants came from the same distribution of a non-difference scenario (p>0.05).

Production of healthy grain per plant was lower in corn plants totally excluded from predators, however these differences were not significantly different from control plants (Table 6-1, p >0.05).

Effect of landscape on biological control of maize pest provided by vertebrate predators. Herbivory (IH) and production of healthy grain (HGW) at harvest time did not differ between enclosed and control plants (Fig. 6-1, p>0.05). Landscape did not affect biological control provided by vertebrates, although herbivory was slightly higher on agricultural landscapes than in forested ones (IH forest mean= 2.22±0.43 vs. IH agricultural mean = 2.36 ± 0.37, p=0.15). Healthy grain weight did not differ between control and enclosed plants neither between landscapes types (HGW agricultural mean = 130.88 ± 124.18 g vs. HGW forest mean = 95.02 ± 72.67g).

Table 6-1. Mean values ± 1 SD for healthy grain weight and damaged grain weight per maize plants in diurnal and nocturnal exclusion predator experiments.

Treatment	Herbivory index (IH)	Healthy grain weight per plant (g)
Control plants	2.08 ± 0.23	119.75 ± 52.23
Diurnal exclusion	2.14 ± 0.58	128.43 ± 51.01
Nocturnal exclusion	2.15 ± 0.45	125.06 ± 77.86
Total exclusión	2.30 ± 0.67	84.88 ± 44.73

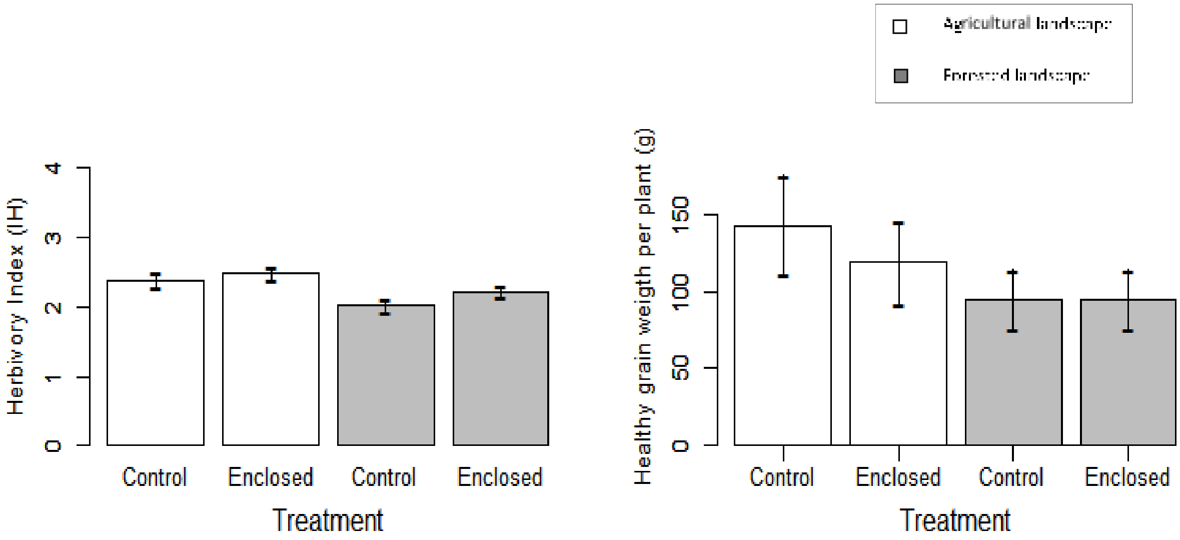

Figure 6-1. Mean and confidence intervals for herbivory index, healthy grain weight per plant and proportion of damaged grain per plant, comparing control plants with the treated plants in agricultural (white bars) and forest landscapes (gray bars).

Assessment of cobs damage by vertebrate herbivores. The damage inflicted by vertebrates to ears tended to be higher in cornfields with higher forest cover around them (Fig. 6-2). Although regression models indicated significant relationships between vertebrate damage and forest cover, perimeter-to-area ratio of each cornfield and altitude, these relationships were no longer significant when an extreme value was excluded from the data (Fig. 6-2).

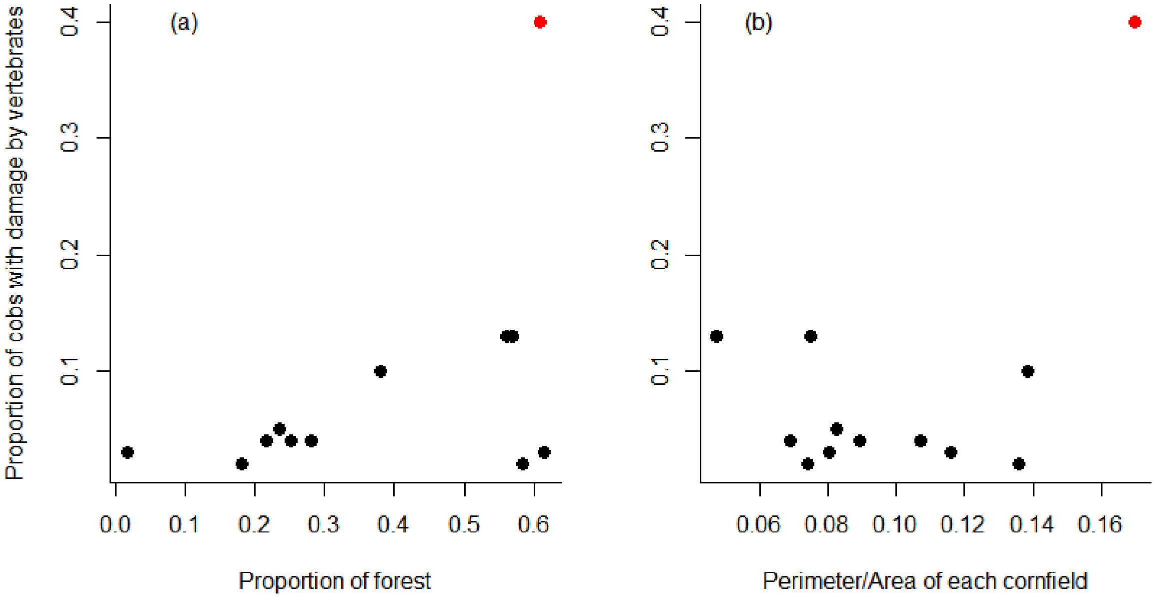

Figure 6-2 Relationships between the incidence of damaged by vertebrates in cornfields, measured as the proportion of cobs with evidence of damage by vertebrates (n=100), and forest cover in a radius of 250 around each field (a), and the perimeter-to-area ratio of each field (b).

Small landholders perceptions of de-faunation. Twenty species of mammals were identified by landholders (Table 6-2). All Carnivora taxa was reported as scarce now and just two species: omnivorous marsupial (*Micoureus regina*) and squirrels (*Microsciurus pucheranii*), were reported as being currently more abundant than 30 years ago. Besides mice and pigeons, five mammal species were identified as herbivores in maize fields: *Microsciurus pucheranii*, *Nasuella olivacea*, *Coendou bicolor*, *Dasyprocta fuliginosa* and *Cebus albifrons malitiosus*.

Table 6-2 Description of mammal species composition in Topaipí (Cundinamarca, Colombia), and small landholders' perceptions concerning their abundance over the last 30 years.

Orden (Family)	Scientific Name	Common name	Perception's abundance
Carnivora (Canidae)	*Cerdocyon thous* (Linnaeus, 1766)	*Fox*	Scarce
Carnivora (Felidae)	*Leopardus tigrinus* (Schreber, 1775)	*Ocelot*	Scarce
Carnivora (Canidae)	*Potos flavus* (Schreber, 1774)	*Kinkajou*	Scarce
Carnivora (Mustelidae)	*Mustela Felipei* (Izor & de la Torre, 1978)	*Otter/Weasel*	Scarce
Carnivora (Procyonidae)	*Bassariscus sumichrasti y Bassaricyon gabbii* (J.A. Allen, 1876)		Scarce
Carnivora (Procyonidae)	*Nasua nasua* (Linnaeus, 1766)		Scarce
Carnivora (Procyonidae)	*Nasuella olivacea* (Gray, 1865)	*Mountain Coati*	Scarce
Didelphimorphia (Didelphidae)	*Micoureus regina* (Thomas, 1898)	*Woolly Mouse Opossum*	More abundant
Phyllophaga (Bradypodidae-Megalonychidae)	*Bradypus variegates* (Schinz, 1825) *y Choloepus hoffmanni* (Peters, 1858)		Scarce
Rodentia (Dasyproctidae)	*Dasyprocta fuliginosa* (Wagler, 1832)	*Black Agouti*	Scarce
Rodentia(Agoutidae)	*Agouti paca* (Linnaeus, 1766)	*Limpet*	Scarce
Cynculata (Dasypodidae)	*Dasypus novemcinctus* (Linnaeus, 1758) y *D. septemcintus* (Linnaeus, 1758)	*Armadillo*	Scarce
Rodentia (Sciuridae)	*Microsciurus pucheranii* (Fitzinger, 1867)*	*Squirrel*	More abundant
Vermilingua (Myrmecophagidae)	*Tamandua tetradactyla* (Linnaeus, 1758) *y T. mexicana* (Saussure, 1860)	*Ant-eater*	Scarce
Rodentia (Erethizontidae)	*Coendou bicolor* (Tschudi, 1844)	*Bicolored-spined porcupine*	Scarce
Primates (Cebidae)	*Cebus albifrons malitiousus,* (Humboldt 1812)	*White-fronted capuchine*	Scarce

Discussion

Role of vertebrates in pest control. Both experiments involving predator-exclusion had the same results in which, no significant difference was observed in herbivory or production between corn plants exposed to vertebrate predators and corn plants located inside enclosures. In the first experiment the herbivory tended to be lower in plants excluded from diurnal and nocturnal predators and higher on plants totally excluded from both predators, however these differences were not significant. Likewise, in the second experiment evaluating the effect of landscape on predation-exclusion experiments herbivory was slightly higher on enclosed plants than in controls but differences were not significant.

Our results are contrary to other predator exclusion studies conducted in other agro-ecosystems in which enclosed plants were reported to have higher pest infestation levels and greater damage than control plants (Aflegrim 1989, Greenberg *et al.* 2000, Tremblay *et al.* 2001, Mols and Visser 2002, Hooks *et al.* 2003, Kellermann *et al.* 2008, Johnson *et al.* 2010). In order to explain why vertebrate predator exclusion did not lead to either an increase in cob damage or crop yield in maize plants, we propose several explanations.

First, it is possible that neither diurnal nor nocturnal vertebrates are effective in controlling the main pest typical of maize crops (*S. frugiperda*), as these particular larvae utilize the whorl as a refuge, or because the larvae, due to their small size, are not ideal sustenance for vertebrate predators. Larvae of *S. frugiperda* are usually located hidden inside the corn whorl, hence, they are not accessible to birds during the larvae stage of their life cycle. Similar findings was reported by Hooks *et al.* (2003) who suggested that caterpillars that attack *Brassica* crops are protected from bird predation inside the inflorescence of these plants, which could serve as a refuge or enemy-free space for this pest. Additionally, the first stage larvae of *S. frugiperda* measures 30 mm long and 4.5 mm wide (Angulo *et al.* 2006) and therefore, they are too small for big predators like birds or bats, which prefer larger size prey (Greenberg *et al.* 2000, Mols and Visser 2002, Hooks *et al.* 2003).

Our second explanation is that mortality inflicted by invertebrates could compensate for the absence of vertebrate predators, given that ants, wigs, spiders and predator beetles were able to enter the enclosures and could have eaten the eggs and larvae of insect pests. Bird exclusion might reinforce the predatory activity of invertebrate predators such as earwigs (Dermaptera: Forficulidae). Earwigs are one of the main predators of eggs and first stage larvae of *S. frugiperda* (Sueldo *et al.* 2010). In addition, earwigs have been noted to be one component in the diet of birds in forest habitats (Pinol *et al.* 2010). In cornfields, this group of predators was always found inside the whorl corn, the same habitat as the *S. frugiperda* larvae. Therefore, enclosures might have protected earwigs from predation from vertebrates and reinforced their role as consumers of eggs and first stage larvae in *S. frugiperda*.

Other predators and parasitoid were also abundant in maize plants, specifically Hymenoptera parasitoids (29 families, 37% of indviduals), spiders (60 morpho species; 19% ofindividuals), predator diptera (3 morpho-species, 13% on individuals) and ants (47 morpho-species, 12% of individuals) (EMP Unpublished data). The overall abundance of these groups of natural enemies had a negative relationship with the richness of leaf-chewer herbivores in the same cornfields (EMP Unpublished data). Therefore, these diverse assemblage of pest's natural enemies could preyed or parasited on *S. frugiperda* eggs and larvae, reinforcing the control of this pest in maize plants inside and outside the enclosures, especially as they are able to capture small and concealed prey. However, the relative importance of invertebrate predators could be diminished by intraguild predation, but we had not data available to test differences in the abundance of predators or herbivores between covered plants and controls.

A third explanation of the results from the predator exclusion experiments is that the abundance of *S. frugiperda* during the time span of the experiments was limited and it does not allow for the appropriate evaluation of the role of vertebrate predators. One evidence to support this hypothesis is that we were unable to capture male moths in our pheromone traps for a period of six weeks during the experiment. In addition, it has been suggested that insectivorous birds and bats (Kunz *et al.* 2011) seek out areas of concentrated prey sources. Therefore, further analysis should consider temporal variation in the population of whorl worms in cornfields in order to establish the periods more critical for pest control, as well as, foraging behavior of vertebrate species.

Finally high habitat heterogeneity also could attenuate top-down control in the studied cornfields. For instance, the first experiment was carried out in a complex habitat, surrounded by 62% of native forest and with a great diversity of weeds inside the field (48 species, Unpublished data). In such complex agroecosystems, the effects of top predators on plants are attenuated through the pass over a complex food web with higher species diversity and many omnivorous species and intra-guild predation (Schmitz *et al.* 2000). Although we had a gradient on forest cover in the landscape that varied from 0% to 62%, this gradient did not affect the richness of weeds, which was high everywhere. Thus habitat heterogeneity due to high richness of weeds prompted the abundance of arthropod natural enemies in the entire landscape (EMP Unpublished data).

The results of predator exclusion experiments did not respond to changes in forest cover around the crops. Differences in herbivory and production of healthy grain per plant between control and enclosed plants behaved according to our expectation of higher damaged in enclosed plants, which in turn translate into lower production in enclosed plants, particularly in cornfields mainly surrounded by agricultural areas. Non-significant differences between control and enclosed plants might had occurred due to the small number of replicates used in this experiment.

Role of vertebrates as herbivores. The average consumption of cobs by vertebrates was 5.72% ±. 4.19% with an extreme value of 45% observed in a cornfield with strong edge effect due to small size area. We also observed a trend to higher press of vertebrates in more forested landscapes, however it depends on other factors such as field size. Thus smaller fields closer to forest suffered more damage by vertebrates such as squirrels and other small mammals.

The perceptions of corn producers suggests that damage inflicted by vertebrate herbivores and particularly squirrels, has increased over the last 30 years. At the same time, producers reported that the potential predator vertebrates of these herbivores have been locally extinct or their abundance has been significantly reduced in the region. The decrease or loss of other predators in agricultural landscapes could explain the increase in damage inflicted by squirrels as reported by producers. Furthermore, this problem was more evident in crop fields located next to native forests. In order to test the de-faunation hypothesis, further research should measure diversity and abundance of insectivorous vertebrate species.

To sum up, a high diverse assemblage of pest's natural enemies in complex agroecosystems may constraint pest control due to complex food webs, in which omnivory and intraguild predation are common. In such system, diurnal and nocturnal predators have an equally important role in pest control in cornfields, and an additive effect on pest-suppression in maize crops. Damage by granivorous vertebrates could be minimized by encouraging conservation of carnivore taxa, meanwhile, the shape and size of the cornfields could be designed in order to reduce granivory performed by vertebrates.

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7. Synthesis

Clearance of forest remnants in the studied crop systems had complex relationships with the diversity of weeds and arthropods within crops. The results clearly support the idea that a simple measurement of diversity, such as, species richness or abundance of species does not capture all this complexity. Therefore, the study of changes in diversity in relation to land-use intensification should consider a wider notion of biodiversity, taking into account: *i)* different spatial scales *ii)* the interaction networks between plant and arthropods, and *iii)* the spatial distribution of species in landscape.

Local diversity

Alpha diversity was high for plants and arthropods in the twelve studied cornfields. The average plant richness per cornfield was 52 ± 14 morpho-species, average herbivore richness was 73 ± 16 morpho-species, average predator richness was 32 ± 8 and parasitoid richness was 17 ± 2 families per cornfield. High dominance of communities of plants and arthropods within cornfields happened regardless of whether the field was mainly surrounded by agricultural covers or by native forest.

Relationship between forest cover and alpha diversity

Classical diversity measures, such as species richness of plants and arthropods, did not show a significant relationship with native forest cover surrounding each cornfield. However, when ‘true diversities’ analysis was applied, plant species of intermediate abundance and abundant predators had a negative relationship with forest cover. Likewise, a functional classification of plants and herbivores species revealed that these groups had differential responses to forest cover. For example, the richness and cover of weeds and low-dominance herbs were positively related to forest cover, while grasses did not respond to changes in this variable

The richness and abundance of leaf-chewers herbivores was positively correlated with the percentage of forest cover, but the rest of arthropod trophic groups did not respond to changes in forest cover around the crops or to other environmental predictors. However, when a network approach was applied, and arthropods were collected directly on corn plants and dominant weeds within each cornfield, a significant and positive realtionship between forest cover and predator richness was observed. Finally, the abundance, but not the richness of parasitoid families was related positively with forest cover.

Other cornfield characteristics, such as the field's previous land-use and the content of soil organic matter influenced within-field plant diversity. Particularly, a strong reduction in plant species richness was observed in conrfields previously dominated by one plant species and in those fields previously covered by pastures and other crops. When a functional characterization of plants was applied, the analysis revealed that negative relationships between field's previous land-use and plant richness were restricted to grasses and low-dominance herbs, but not weeds. However, weed coverage was reduced significantly in these cornfields. These results support the idea that local factors such as crop management practices and the legacy of previous land use of the cornfield may play a central role in the assemblage of weed communities in crops. Therefore, plant diversity in each field may reflect the composition and size of the seed bank, which in turn is mainly affected by field management (Franke *et al.* 2009).

Local diversity of arthropods was higly dependent on the availability of their resources. For instance, herbivore richness was positively related to plant species richness, regardless the order of diversity considered. Nonetheless, the responses of herbivores to plant diversity varied between leaf-chewer and sap-feeder species. Only sap-feeder richness was positively related to weed and low-dominance herbs, whereas leaf chewer richness was related only to forest cover.

The responses of arthropods to plant diversity varied among trophic groups and were dependent on plant dominance. For instance, the richness of weeds was negatively related to the abundance of predator but it was positively related to parasitoid abundance. Likewise, the abundance of herbivores was negatively related to the richness of weeds, but was positively related to the richness of grasses and low-dominance herbs. Therefore, a deeper knowledge of the trophic interaction between plants, herbivores and predators is needed to understand the contribution of plant diversity to pest control.

Plant-arthropod networks

Dominant weeds within cornfields play a central role structuring the communities of herbivores. Plants and arthropods within cornfields were organized in a strong modular structure, with plants acting as module hubs and arthropods, particularly herbivores, being peripheral nodes. High modularity in arthropod-plant interaction networks suggests that herbivores exhibit high specialization in host plant preferences, which was indicated by the lower number of average links per species (1.2 ± 0.1).

Forest cover in the landscape and weed richness within the cornfield influenced network size, as well as, the average number of links per species and modularity. Larger networks more connected and less compartmentalized were observed in cornfields with larger forest cover around them. The trend of higher modularity in more altered landscape suggests that herbivores may change their use of resources, focusing in lower number of species as the cover of forest decreases, a trend previously documented in agroecosystems (Tylianakis *et al.* 2007).

Between field diversity

Weed and predator assemblages had a higher turnover of species between cornfields in the landscape. Although each cornfield community was highly dominated by few species, different species dominated each cornfield. Higher values of beta diversity were observed among dominant plants and among rare species of predators. Furthermore, forest cover influenced changes in plant species composition among cornfields. The results suggest that the structure of weed communities depended on local factors, such as historical use of fields, composition of seed bank and soil characteristics, as well as, on landscape factors e.g. the cover of forest.

Changes in beta diversity in weeds and arthropods were not related to geographical distance between cornfields. This results suggest that dispersion capacity of species has less importance than species interactions in structuring these communities. Only turnover of herbivores species responds to gradients in forest cover and gradients in plant species richness, which add evidence to the central role that forest cover and weed richness play in the organization of herbivore assemblages within the cornfields.

Plant and arthropod meta-communities were nested, which indicates that species composition of cornfields holding fewer species are subsets of those fields holding more species. Nestedness in plants was mainly explained by altitude and content of organic carbon in soils, but not by forest cover. This result suggests that colonization of cornfields by plant species may depend more on field characteristics and crop management practices than on landscape configuration. Nestedness in arthropod meta-communites was explained mainly by gradients in forest cover surrounding the crops as well as by plant richness. This finding confirms the strong bottom up controls in this agroecosystem, in which plant diversity prompted herbivore and natural enemy diversity.

Relationships between forest cover, biodiversity and crop production.

Native forest influenced ecological essential processes in corn yield. On one hand forest cover indirectly enhances herbivory in corn plants by maintaining more diverse assemblages of leaf-chewers herbivores –the main factor associated with herbivory-. On the other hand forest cover enhances crop yields through its positive effects on interaction networks, in which cornfields with diverse assemblages of predator had higher crop yields. Thus, the relative importance of native forest on pest control and production in traditional cornfields depends on the balance of those two effects. Pest control in traditional cornfields in this locality has been long dependent exclusively on biological pest control, and supported by the lower levels of whorl worms measured at field, it is likely that the positive effects of native forest on pest´s natural enemies overcome their negative effect through increased diversity of leaf-chewer herbivores.

Classification of plants and herbivores in relevant categories for pest managements provided valuable insights into exploring the functional role of these groups in the agroecosystem. The richness of grasses may enhance pest regulation cornfields, as suggested by their positive relationship with the richness of leaf-chewer herbivores, but a negative relationship with the damage inflicted to corn plants by whorl worms (*Spodoptera frugiperda* and *Copitarsia decolora*). These insects are a major pest in corn crops in other areas, but in the study area their populations still lower across all crop season. In addition, a feeding preference for grasses has been reported to these species, thus it is likely that higher diversity of grasses within cornfields may help regulate their populations via associational resistance (Barbosa *et al.* 2009).

Conclusion

To sum up, weed richness had strong bottom-up control of herbivores and pest´s natural enemies in traditional cornfields, which in turn translate into herbivory and corn yield. In the studied cornfields pest control was provided by native predators and parasitoids, which in turn depended upon the maintenance of the diversity of weeds within crops. Forest cover promoted complexity of networks of plant-arthropod in this system, in which the richness of predators was associated with an increased production of crops. Therefore, the conservation of forests in traditional crop systems is essential for biological control, production and biodiversity conservation.

The traditional cornfields studied are a good example of sustainable agriculture, given that production of corn is carried out with minimum external inputs and pest regulation is achieved by maintaining an outstanding diversity of plants inside the cornfields. Management of pest and weeds are based on local knowledge, by avoiding to sow corn during months with higher pest pressure and by controlling weeds in critical stages of the crop. This crop system resembles natural ecosystems in different ways, such as high diversity, complex interactions between components, and reduced loss of nutrients

Recommendations

This work provides basic knowledge about the patterns of biodiversity in traditional agroecosystems, which could be useful for future research on pest management strategies based on native biodiversity. On one hand, our results add evidence to the hypothesis that plant diversity within plots is essential to support more abundant and diverse assemblages of pest’s natural enemies. On the other hand, our data also confirmed that a functional characterization of diversity is needed to gain insights into understanding how this vegetation diversity enhances pest control in crops. For instance, low-dominance herbs, but not weeds or grasses were positively associated with most diverse assemblages of predators.

More detailed analysis of composition of plant-arthropod networks could provide information that enables us to detect native plants that shared herbivores with corn plants, as well as, native plants that host more abundant and diverse assemblages of predators and parasitoids. Such information is fundamental for biological control and to design pest management strategies such as trap plants (Shelton and Badenes-Perez 2006), repellent plant and push-pull strategies (Midega *et al.* 2008, Khan *et al.* 2011), which are based on specific ecological and behavioral knowledge of preference-performance of herbivores on their host plants (Poveda *et al.* 2008, Finch and Collier 2012). In such context, we recommend to focus on grasses to carry on experiments in preference-performance for major pest in corn crops, such as *S. frugiperda* and *C. decolora*, given that the damage inflicted by these whorl worms to corn plants was negatively related to grass richness.

The studied agroecosystem is highly vulnerable to habitat disturbance. Firstly, habitat heterogeneity induces strong turnover of species for plants and arthropods, which means that ecosystem functioning in this landscape depends on a diverse assemblage of organisms, more than in few dominant highly effective species. Second, along with pest control, other ecosystem services strongly depend on low-input management of cornfields. For instance, soil fertility, water infiltration and control of flooding are maintained by reducing tillage, a permanent cover of weeds and a relatively closed nutrient cycling, given that crop litter remain in the plot after harvest. Thus, the ecological structure of this agroecosyems, as well as their agronomic properties depends on the preservation of farmer's local knowledge and its traditional agricultural practices.

Furthermore, farmers' perception of vertebrate diversity indicates that besides production, this landscape is able to preserve wild fauna through preserving remnants of native forest. The damaged inflicted by vertebrates in cornfields can be controlled by reducing edge effects. Thus the producer should avoid to grow corn in small fields (e.g. 500-1000 m^2) mainly surrounded by forest. Moreover, environmental education programs should carry on to stop de-faunation of forest, promoting the conservation of small predator species, which in turn could enhance control of rodent species that attack cornfields.

Further research is needed to understand how biodiversity in complex landscapes is maintained, besides the intensity of local management. We hypothesize that field borders, hedgerows, way/road borders and fallows prompted process such as dispersion and colonization of organism across the landscape. However, we recommend focusing on habitat suitability for each group of organisms, more than on the effects of classical landscape metrics to study the effects of habitat loss and landscape configuration on biodiversity.

Finally, our results could be used by decision-makers in order to define payments for provision of ecosystem services to farmers who produce food in a sustainable way. We consider that the studied municipality fulfills all conditions for access to some system of ecological certification in good agronomic practices, in order to improve the income of farmers and to support familiar agriculture in marginal areas. Thus, agroecological research with a participatory focus should be done in this area, in order to get benefits from biodiversity to poorest farmers and to continue preserving such diversity.

In addition, we hope that our results help farmers to change their perceptions about forest in agricultural landscapes, in a way that the presence of forest in farm increases the commercial value of farms instead of reducing it. Thus, the conservation of remnants of native forest is only possible through the social acceptance of their utilitarian and non-utilitarian value for all sectors in society.

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Appendixes

Appendix 3.1 Results of linear regression models for biodiversity of plants and five field characteristic measures in twelve traditional cornfields located in the Colombian Andes. Coefficient values of predictor variables and p-values are shown for significant effects, at a 90% confidence level.

Response variable	Forest cover	Field perimeter-to-area ratio	Soil organic carbon	Altitude	Former land-use				Explained variance
					Crops	Pastures	Fallow	Biological invasion	
Diversity of plants ^0D	n.s.	n.s.	0.15 P=0.07	n.s.	-0.43 P= 0.04	-0.47 P= 0.04	n.s.	-0.69 P= 0.0001	75%
^1D	-0.16 P= 0.047	0.29 P= 0.002	n.s.	n.s	-0.91 P= 0.014	-0.67 P= 0.025	-0.82 P= 0.004	-2.24 P<0.0001	89%
^2D	n.s.	0.23 P=0.028	n.s.	n.s.	n.s.	n.s.	-0.86 P=0.016	-2.45 P<0.0001	92%

Appendix 3.2. Results of linear regression models for biodiversity of plants and six field characteristic measures in twelve traditional cornfields located in the Colombian Andes. Coefficient values of predictor variables and p-values are shown for significant effects, at a 90% confidence level.

Response variable	Forest cover	Altitude	Field perimeter-to-area ratio	Diversity of plants			S. O. M.	Former land-use of the cornfield				Explained variance
				^0D	**^1D**	**^2D**		**Crops**	**Pastures**	**Fallows**	**Biological invasion**	
Herbivores												
^0D	n.s.	n.s.	n.s.	n.s.	0.19	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	76.5%
					P<0.0001							
^1D	n.s.	n..s.	n.s.	n.s.	0.24	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	46.0%
					P<0.0001							
^2D	n.s.	-0.16	n.s.	n.s.	0.27	n.s.	n.s.	n.s	n.s.	n.s.	n.s	49.6%
		P=0.064			P= 0.003							
Predators												
^0D	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	
^1D	n.s.		0.19	n.s.	n.s.	n.s.	n.s	-0.98	n.s.	-0.49	-1.43	73.6%
			P=0.042					P=0.007		P=0.08	P=0.0002	
^2D	-0.314	n.s.	0.71	-0.46	n.s.	n.s	n.s	-3.04	-2.09	-2.54	-5.34	97.3%
	P=0.065		P=0.011	P=0.029				P=0.0009	P=0.0118	P=0.0063	P=0.0031	

Appendix 4-1. Results of regression models analyzing relationships between networks's metrics and environmental descriptor of cornfields. Values represent coefficients of each factor and asterisks indicate their significance: *P <0.05, **P <0.01, ***P <0.001.

Network's metrics	Forest cover	Plant richness	Altitude (m)	Field size (m^2)	Variance explained
Network-size:					
Total arthropod richness	0.100*	0.104*	n.s.	n.s.	Null deviance= 21.45 (df=11
					Residual deviance = 10.86 (df=9)
Herbivores richness	0.113*	0.212*	n.s.	n.s.	Null deviance= 26.45 (df=11
					Residual deviance = 8.73 (df=9)
Predator richness	0.211*	n.s.	n.s.	n.s	Null deviance= 28.29 (df=11
					Residual deviance = 22.54 (df=10)
Average links per species	0.046*	n.s.	n..s.	n.s.	R^2 = 0.59, F(2,9)= 8.83**
Standardized modularity	-0.028**	n.s.	n.s.	n.s.	R^2 = 0.69, F(2,9)= 17.54**

Appendix 4-2. Results of regression models analyzing relationships between herbivory, networks's metrics and other environmental descriptor of cornfields. Values represent coefficients of factors that remained significant after a forward simplification procedure. Asterisks indicate their significance: *P <0.05, **P <0.01, ***P <0.001.

Factor	Coefficient
Herbivory index	-30.43*
Predator richness	28.98 *
Forest cover	n.s.

Adjusted R-squared: 0.5176, F-statistic: 4.934 on 3 and 8 DF, p-value: 0.0316

Appendix 4-3. Results of regression models analyzing relationships between crop yield, networks's metrics and other environmental descriptor of cornfields. Values represent coefficients of factors that remained significant after a forward simplification procedure. Asterisks indicate their significance: *P <0.05, **P <0.01, ***P <0.001.

Factor	Coefficient
Herbivore richness	3.21 **.
Average number of links per specie plant (g)	n.s.
Overall plant richness	-0.28*
Altitude	n.s.

Adjusted R-squared: 0.6892, F-statistic: 5.878 on 5 and 6 DF, p-value: 0.02609

Appendix 5-1 Composition and relative coverage of plants registered in twelve traditional cornfields in the Colombian Andes.

Family	Relative Coverage (%)	Family	Relative Coverage (%)
Poaceae	16.24	Cucurbitaceae	0.36
Asteraceae	11.94	Lythraceae	0.31
Dennstaedtiaceae	10.70	Sterculiaceae	0.29
Cyperaceae	7.44	Oxalidaceae	0.28
Zingiberaceae	6.39	Cecropiaceae	0.28
Euphorbiaceae	4.92	Melastomataceae	0.27
Balsaminaceae	3.95	Phytolaccaceae	0.27
Araceae	3.82	Heliconiaceae	0.19
Commelinaceae	3.50	Onagraceae	0.16
Caryophyllaceae	3.35	Piperaceae	0.15
Lamiaceae	3.12	Caesalpiniaceae	0.12
Rubiaceae	2.85	Cannaceae	0.12
Amaranthaceae	2.32	Mimosaceae	0.11
Apiaceae	1.80	Ptridaceae	0.08
Solanaceae	1.58	Apocynaceae	0.08
Malvaceae	1.43	Selaginellaceae	0.08
Urticaceae	1.36	Brassicaceae	0.07
Vitaceae	1.24	Rosaceae	0.05
Boraginaceae	1.21	Myrtaceae	0.05
Convolvulaceae	1.19	Begoniaceae	0.02
Fabaceae	1.05	Aspleniaceae	0.01
Thelypteridaceae	1.04	Iridaceae	0.01
Scrophulariaceae	1.02	Eriocaulaceae	0.01
Blechnaceae	0.67	Ochnaceae	0.01
Acanthaceae	0.64	Chenopodiaceae	0.00
Verbenaceae	0.61	Not identified	0.81
Menispermaceae	0.46		

Appendix 5-2. Composition and relative abundance of herbivores, predators and parasitoids collected in twelve traditional cornfields in the Colombian Andes.

HERBIVORES		PREDATORS		PARASITOIDS	
Family	Rel. ab. (%)	Family	Rel. ab. (%)	Family	Rel. ab. (%)
Cicadellidae	47.30	Dolichopodidae	21.08	Syrphidae	12.02
Chrysomelidae	17.24	Formicidae	15.68	Pteromalidae	11.87
Miridae	11.00	Araneidae	12.20	Eulophidae	6.79
Tettigoniidae	5.46	Tetragnatidae	11.29	Scelionidae	6.71
Acrididae	5.09	Empididae	8.38	Phoridae	5.46
Bruchidae	2.51	Linyphiidae	3.90	Cynipidae	5.39
Agromyzidae	1.52	Silvanidae	3.82	Figitidae	4.53
Eumastacidae	1.32	Berytidae	3.49	Chalcididae	3.59
Delphacidae	1.19	Reduviidae	2.74	Ichneumonidae	2.97
Gryllidae	1.10	Theridiidae	2.49	Encyrtidae	2.73
Largidae	0.77	Staphylinidae	2.41	Eurytomidae	2.65
Tetrígidae	0.65	Lycosidae	2.16	Diapriidae	2.42
Curculionidae	0.62	Thomisidae	1.91	Perilampidae	1.64
Dictyopharidae	0.49	Salticidae	1.58	Tachinidae	1.64
Tephritidae	0.47	Oxyopidae	1.49	Mymaridae	1.48
Membracidae	0.45	Forficulidae	1.08	Crabronidae	1.17
Tingidae	0.45	Vespidae	1.08	Platygastridae	1.09
Cixiidae	0.40	Scydmaenidae	0.58	Ceraphronidae	0.94
Anobiidae	0.33	Cantharidae	0.41	Bethylidae	0.62
Otitidae	0.23	Coccinellidae	0.41	Eucharitidae	0.62
Platystomatidae	0.20	Carabidae	0.25	Torymidae	0.31
Aphididae	0.18	Pompilidae	0.25	Agaonidae	0.23
Cercopidae	0.15	Mysmenidae	0.17	Liopteridae	0.23
Lygaeidae	0.15	Nesticidae	0.17	Sierolomorphidae	0.23
Cecidomyiidae	0.12	Pselaphidae	0.17	Eupelmidae	0.16
Coreidae	0.10	Theridiosomatidae	0.17	Evaniidae	0.16
Lonchaeidae	0.08	Anyphaenidae	0.08	Monomachidae	0.16
Psyllidae	0.07	Asilidae	0.08	Pipunculidae	0.16
Thyreocoridae	0.07	Cicindellidae	0.08	Proctotrupidae	0.16
Pentatomidae	0.05	Cleridae	0.08	Tiphidae	0.16
Elateridae	0.03	Lampyridae	0.08	Trichogrammatidae	0.16
Fulgoridae	0.03	Sparassidae	0.08	Ormyridae	0.08
Oedemeridae	0.03	Sphecidae	0.08		
Pyrrocoridae	0.03	Not identified	0.08		
Rhyparochromidae	0.03				
Cerambycidae	0.02				
Mordellidae	0.02				
Tenthredinidae	0.02				

Appendix 5-3. Results of generalized linear models (Poisson regression) with a stepwise forward simplification of the richness and abundance of weeds, grasses and native plants, collected in tradition cornfields in the Colombian Andes, in relation to native forest cover in a 250 m radius around the crop and other environmental predictors such as altitude, perimeter-to-area ratio of each cornfield, percentage of soil organic carbon, as well as to the richness of weeds, grasses and native plants. Values correspond to coefficient of each factor in the model and p-values when the relationship was significant

					Previous use of each cornfield				
Group	Forest cover	Field perimeter -to-area ratio	Soil organic carbon (%)	Altitude (m)	Other crops	Pasture	Secondary growth	Invaded fields	Explained variance
PLANT RICHNESS									
Pooled data	n.s.	n.s	0.15	n.s.	-0.43	-0.47	n.s.	-0.69	Null deviance: 40.6 (11 d.f.)
			P=0.0738		P=0.0423	P=0.0471		P=0.0001	Residual deviance: 10.1 (5 d.f.)
Weeds	n.s.	n.s.	0.10	n.s.	n.s.	n.s.	n.s.	n.s.	Null deviance: 12.1 (11 d.f.)
			P=0.0916						Residual deviance: 9.4 (10 d.f.)
Grasses	n.s.	n.s.	n.s.	0.22	n.s.	n.s.	-0.80	-0.97	Null deviance: 25.1 (11 d.f.)
				P=0.1111			P=0. 0399	P=0.0504	Residual deviance: 4.4 (6 d.f.)
Low-dominance herbs	n.s.	n.s.	n.s.	0.14	-0.43	n.s.	n.s.	-0.92	Null deviance: 34.3 (11 d.f.)
				P=0.0473	P=0.0507			P<0.0001	Residual deviance: 8.4 (6 d.f.)
PLANT COVERAGE									
Weeds	0.05	0.07	0.59	0.05	-1.15	-1.07	-0.37	-0.13	Null deviance: 3063.5 (11 d.f.)
	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001	P<0.0001	Residual deviance: 1193.5 (3 d.f.)
Grasses	n.s.	0.37	0.18	-0.04	-1.33	n.s.	-1.79	-0.6	Null deviance: 5083.1 (11 d.f.)
		P<0.0001	P<0.0001	P=0.0199	P<0.0001		P<0.0001	P<0.0001	Residual deviance: 2580.3 (4 d.f.)
Low-dominance herbs	0.07	n.s.	-0.29	n.s.	0.78	0.38	0.22	-1.07	Null deviance: 1701.2 (11 d.f.)
	P<0.0001		P<0.0001		P<0.0001	P<0.0001	P<0.0001	P<0.0001	Residual deviance: 317.14 (5 d.f.)

Appendix 5-4. Results of generalized linear models (Poisson regression) with a stepwise forward simplification of the richness and abundance of herbivores, predator and parasitoids collected in tradition cornfields in the Colombian Andes, in relation to the percentage of native forest in a 250 m radius around the crop and other environmental predictors such as altitude, perimeter-to-area ratio of each cornfield, percentage of soil organic carbon, as well as to the richness of weeds, grasses and native plants. Values correspond to coefficient of each factor in the model and p-values when the relationship was significant.

Group	Forest cover	Field perimeter-to-area ratio	Soil organic carbon	Altitude	Weeds	Grasses	Low-dominance herbs	Explained variance
HERBIVORE RICHNESS								
Pooled data	n.s.	n.s.	n.s.	n.s.	0.14	n.s.	0.07	Null deviance: 37.6 (11 d.f.)
					P<0.0001		P=0.0562	Residual deviance: 12.5 (9 d.f.)
Leaf'chewer herbivores	0.16	n.s.	n.s.	n.s.	n.s.	n.s.	n.s	Null deviance: 22.0 (11 d.f.)
	P=0.0064							Residual deviance: 14.5 (10 d.f.)
Sap feeders	n.s.	n.s.	n.s.	n.s.	0.24	n.s.	0.09	Null deviance: 43.5 (11 d.f.)
					P<0.0001		P=0.0556	Residual deviance: 8.3 (10 d.f.)
NATURAL ENEMY RICHNESS								Null deviance: 21.3 (11 d.f.)
Predators	n.s.	n.s.	n.s.	n.s.	n.s.	n.s	0.16	Residual deviance: 11.5 (10 d.f.)
							P=0.0016	
Parasitoids	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	
HERBIVORE ABUNDANCE								
Pooled data	-0.11	0.36	0.05	-0.46	-0.24	0.26	0.58	Null deviance: 781.3 (11 d.f.)
	P<0.0001	P<0.0001	P=0.0238	P<0.0001	P<0.0001	P<0.0001	P<0.0001	Residual deviance: 194.9 (4 d.f.)
Free-living chewers	n.s.	0.21	-0.07	-0.55	-0.34	0.30	0.52	Null deviance: 522.7 (11 d.f.)
		P<0.0001	P=0.046	P<0.0001	P<0.0001	P<0.0001	P<0.0001	Residual deviance: 230.2 (5 d.f.)
Sap feeders	-0.13	0.44	0.10	-0.45	-0.22	0.32	0.56	Null deviance: 647.9 (11 d.f.)
	P<0.0001	P<0.0001	P=0.0007	P<0.0001	P<0.0001	P<0.0001	P<0.0001	Residual deviance: 211.9 (4 d.f.)
NATURAL ENEMY ABUNDANCE								
Predators	n.s.	n.s.	n.s.	n.s.	-0.05	0.16	n.s.	Null deviance: 57.0 (11 d.f.)
					P=0.101	P<0.0001		Residual deviance: 32.6 (9 d.f.)
Parasitoids	-0.18	n.s.	-0.25	-0.14	0.38	0.25	n.s.	Null deviance: 294.9 (11 d.f.)
	P<0.0001		P<0.0001	P=0.0019	P<0.0001	P<0.0001		Residual deviance: 72.1 (6 d.f.)

Appendix 5-5. Summary of regression models with a stepwise forward simplification of foliar herbivory and crop infestation level by whorl worms, measured in tradition cornfields in the Colombian Andes.

Dependent variable	Independent variables	Coefficient	p-values	Model fit
Herbivory index	Richness of leaf-chewer herbivores	2.36	0.0199	R^2=0,67
	Abundance of Predators	0.23	0.0132	F(4,7)=6.61, p=0.015
	Perimeter-to-area ratio of each cornfield	0.18	0.0373	
	Coverage of weeds	0.15	0.0638	
Crop infestation level by whorl worms (%)	Richness of leaf-chewer herbivores	0.59	0.00041	Pseudo R^2= 0.5917
	Richness of grasses	-0.53	0.0021	Phi coeff. 17.81, p=0.0367