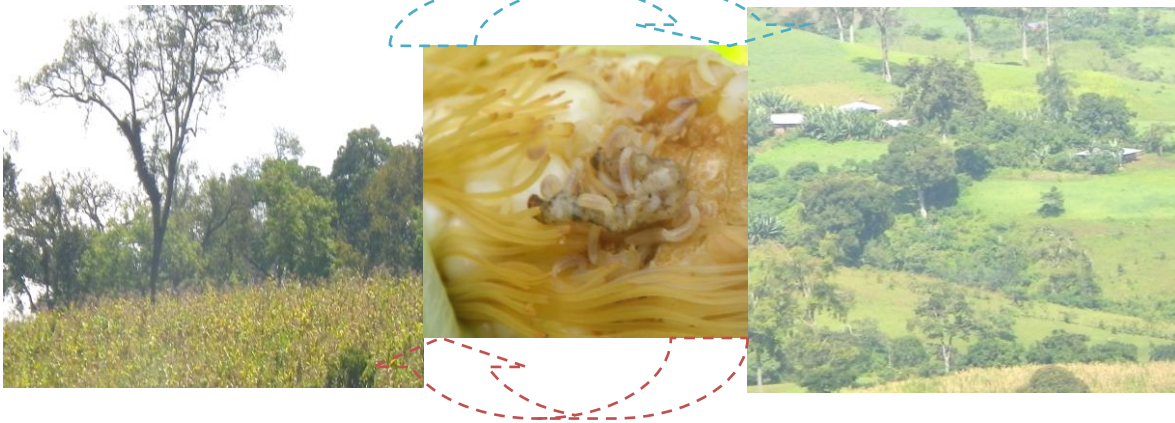


Crop pests and Natural Enemies in Agricultural Landscapes in Relation to Spatial Heterogeneity of Wild Trees and Forests

Debissa Lemessa



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Cover: Wild trees, forest edge and maize crop, pest and parasitoid in Gomma-Gera landscape,
Ethiopia.

Photo by Debissa Lemessa

Summary

The conversion of natural habitat for human use such as, agricultural intensification and others cause the simplification of landscape and loss of biodiversity. The fragmentation of landscape may influence the ecological functions like trophic cascades or predator-prey-primary producer interactions either directly or indirectly. This paper presents the review of the major theories in population regulation, island biogeography, and general concepts in brief and some reports of research findings in trophic cascades, population dynamics of natural enemies in agricultural landscape in both temperate and tropical contexts. The result of the review indicated that the heterogeneity of agricultural landscape (e.g. from simple crop habitat to complex natural habitat) determines not only the cross-edge spillover but also affects the magnitude (abundance), direction of flow and diversity of natural enemies and crop pests. As a result, the efficiency of natural regulation of crop pests in top-down and bottom-up processes may vary accordingly. Nevertheless, from the literature I have assessed, I would suggest that further empirical research is needed to get a comprehensive understanding concerning the relationship between natural pest regulation functions (top-down and bottom-up mechanisms) and crop pests in agroecosystem both at local and regional scales. This suggestion may be vital mainly in tropical regions context where the high biodiversity is declining rapidly on one hand and where little information is currently available on the other verge.

Sammanfattning

Omvandlingen av naturliga biotoper till produktionsmark t.ex. genom intensifiering av jordbruket orsakar en förenkling av landskapet och förlust av biologisk mångfald. Landskapets fragmentering kan påverka ekologiska funktioner antingen direkt eller indirekt som fortplantar sig genom trofinivåerna. Denna uppsats ger en översikt över de huvudsakliga teorierna rörande populationsreglering och ö-biogeografi samt tar upp allmänna begrepp och forskning som har att göra med trofiska kaskadeffekter samt populationsdynamik av arter som livnär sig på skadegörare av grödor i både tempererade och tropiska klimat. Den information som jag har sammanställt antyder att jordbrukslandskapets heterogenitet bestämmer inte bara rörelsen mellan naturliga biotoper och jordbruksmark av skadegörare och dess naturliga fiender utan även mängden och mångfalden av dessa. Som ett resultat av detta så kan naturlig reglering av skadegörare variera. Av vad jag har läst drar jag dock den slutsatsen att ytterligare studier behövs innan vi tillfullo kan förstå sambandet mellan de processer som styr naturlig reglering av skadegörare (inklusive top-down och bottom up mekanismer) i jordbrukssystem lokalt och regionalt. Detta kan få stor betydelse särskilt i tropikerna där den biologiska mångfalden minskar snabbt och den tillgängliga kunskapen ofta är knapp.

Keywords: — Agroecosystem, Biodiversity, Bottom-up, Diversity, Fragmentation, Landscape, Natural enemies, Pests, Top-down population regulation.

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Introduction

Habitat loss and fragmentation have caused the disruption of biological interactions, for example, natural pest control functions in agroecosystems. The change of the landscape by fragmentation has also resulted in the isolation of species into small subpopulations and a change of the community structure (With et al. 2002). In most cases, human land use is responsible for such kind of trend. Agriculture causes the simplification of the landscape as a result of extensive and intensive monoculture cropping system. Ninety percent of the world's cropland is under annual monocultures of mainly wheat, rice, maize, cotton, and soybeans (Altieri and Nicholls 2004). Such agricultural systems are vulnerable to pests and diseases. The definition of pest is an organism that causes harm or damage to man and his possessions and hence from agricultural point of view it could be, for example, an animal (mammal and insect) or fungus that damages the crops. Basically, crop pests comprise of herbivores, frugivores, seed-eaters, and pathogens (fungal, bacterial and viral diseases) that decrease the productivity and sometimes cause a considerable crop loss.

Traditionally, human beings had started to gain knowledge about insects and crop pests during pre-historic times from common insects like bees, termites and silkworms. Since the eighteenth century, humans have used chemical, mechanical, biological controls and integrated pest management (IPM) to protect the crops from pests (Nair 2007). According to Altieri and Nicholls (2004) during the past forty years it was observed that the yield loss due to crop pests was about 20 to 30 percent for most crops and, as a result, the use of pesticides shows an increasing trend in 1995, and accounted to 4.7 billion pounds worldwide. Therefore, the problem that comes from pests is not only the crop loss but also the pollution of the environment from the intensive use of pesticides. Revenue loss from insect pests and pathogens can be disproportionately high for some crops which are sold in fresh condition and for which their price is dependent on such quality (Babcock et al. 1992). Paradoxically, in recent decades pesticide use has led certain species to develop resistance to specific pesticide compounds, triggering pest outbreaks and resurgence.

Similarly, as pointed out by Zhang et al. (2007), at different spatial scales (local, regional and global) the pests may affect the farmers' crop farming systems and crop growing preferences. Therefore, the aim of this paper is to review the research reports on the dynamics of the natural enemies in relation to crop pests in heterogeneous agricultural landscape and to suggest the existing knowledge gap in the area for further research.

Population Regulation

There have been hot debates over the concept of population regulation in ecology (Sinclair 1989, cited in Krebs 2001) mainly on the distinction between terms such as “population limiting factors” and “population regulation factors”. The argument here is that a limiting factor refers to a factor that causes a change in average density of the population. For example, a disease could be a limiting factor for a deer population if deer abundance is higher when the disease is absent. On the other hand, a factor is a regulating factor if the percentage mortality caused by the factor increases with the density of the population. If we take the same example of disease factor, it could be a regulating factor only if it causes an increased loss in population of deer as the density increases. However, for this review purpose I will use the phrase population regulation as it was used in Krebs (2001). In fact, there are several factors which influence the population growth and population size of both plants and animals— within and between populations. Age structure, density and intrinsic rate of survival fecundity and biological control (e.g. trophic interactions) are some of the factors governing the population growth and size. How fast the population is growing depends on the proportions of individuals in each age class. Similarly, the size of the population is density - dependent. This is because the space and the availability of food have profound importance for the regulation of the population size. In addition, other factors, such as predators, parasitoids, parasites and diseases which have stronger impacts on crowded population than in less densely populated ones (Ricklefs 2007).

Bottom-up and Top-Down Control

Since the early 20th century, theoretical advances have paved the way for the ecologists to undertake several findings and understand how populations are regulated from below or above in biological communities at ecosystem level. In most ecosystems, plants form the base of the food chains and their productivity directly and indirectly influence all higher trophic levels. This resource is the underlying force for bottom-up regulation of the populations in higher trophic levels. Hence, bottom-up regulation is strong where density dependent mortality prevails due to shortage of food. The bottom-up theory was developed before Hairston et al. (1960) introduced the top-down concept stating that predators protect the “green world” from herbivores (e.g. rabbits and sea urchins), through regulating their density or population size from reaching the outbreak level and hence when the predators limit the consumers the primary producers will flourish.

According to Terborgh et al. (2010) bottom-up control is necessary for the flow of resources in to the system while top-down control is important for the distribution of the resources among trophic levels. Human land-use since long time ago has affected the growth of the primary producers and altered the interaction of the communities within and between the ecosystems. Loss of habitat and degradation, crop fertilization, insecticide use, wildlife conservation and algal blooming are some of the major examples of human management that cause challenges to critically understand the current interactions between bottom-up and top-down population regulation in ecosystems (Borer and Gruner 2009). The concept of top-down and bottom-up processes or interactions of biological communities could be described in a path analysis as shown in Fig. 1.

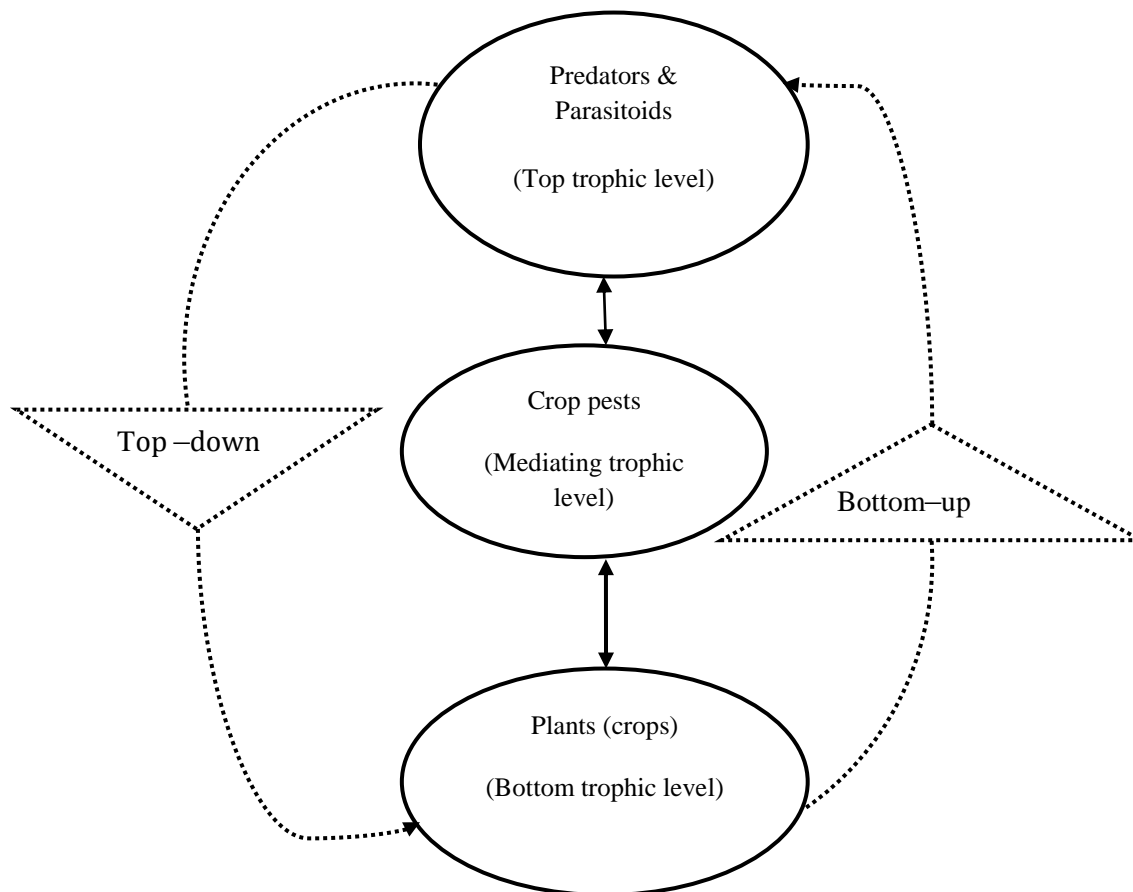


Figure 1. Top-down and Bottom-up population regulation mechanisms (modified from Kagata Ohgushi 2006).

As illustrated in Fig.1, insect population dynamics could be governed in both ways by bottom-up (producers mediated) and by top-down (predators and parasitoids -mediated) processes and with the interactions between them (Daugherty et al. 2007). The underlying science of bottom-up and top-down mechanisms and their role in trophic cascades could be described in more as follows taking some specific examples. Here, trophic cascade means the indirect effect of predators in the successive lower trophic levels. To illustrate the top-down trophic cascade in aquatic systems, Borer and Gruner (2009) used the example of phytoplankton as primary producers. Phytoplanktons are grazed by zooplanktons (e.g. *Daphnia* spp.) which in turn are consumed by small planktivorous fish (e.g. minnows). Accordingly, planktivorous fish is at a third trophic level limiting the population of zooplankton (second trophic level) and releases phytoplankton-primary producers. The terrestrial top-down trophic cascade could be demonstrated from Sinclair et al. (2010) in African savanna where the top predator (e.g. lion) regulates the population of the ungulates so

that the grass biomass will be enhanced in national parks. Both examples include three trophic levels. There are also cases where there are intermediate predators (e.g. hyena, wolves) between top predators (e.g. lion) and herbivores (e.g. small ungulates such as Oribi, impala, topi etc...). Species in such interactions are both consumers and resources for other consumers.

Furthermore, Garibaldi et al. (2010) indicated that bottom-up and top-down processes interactively control food web dynamics in that top-down control would increase with resource availability to plants, while bottom-up control would be stronger under low predator abundance. These effects are both direct and indirect and the bottom-up control starts from abiotic components, such as soil fertility that affects the primary producers and the successive higher trophic level, for example, predators (Levin 2009). Forkner and Hunter (2000) has proposed some predictions from synthesizing previous findings that (1) top-down and bottom-up regulation vary in space and time and their interaction determines population sizes of intermediate trophic-level species; and (2) the strength of top-down control will increase with increasing primary productivity. Moreover, the importance of environmental variation and species identity as important mediators of top-down and bottom-up regulation was also reported by Forkner and Hunter (2000).

Island Biogeography

Island biogeography refers to the presence and absence of species on islands and how the colonization and extinction of species affect the structure of biological community. The equilibrium theory of island biogeography which was developed during 1960s by McArthur and Wilson states that the number of species on island exists as a balance between colonization of new immigrant species to island and extinction of formerly inhabited species on islands. When the number of species increases on island, the rate of immigration of new species decreases and as a result fewer immigrants of new species could be found on the island. On the other hand, if the number of species increases on an island, the rate of extinction increases. This shows that the colonization and extinction rates will lead the number of species to attain a steady state at a certain level. This theory has also further elucidated taking the size of islands and the distance from mainland (source of the species). Small islands support fewer numbers of species than large islands due to a low immigration rate on small islands, but there are also higher competition and extinction rates on smaller

islands than on larger islands. In terms of distance from the source pool, islands near the mainland have more species than those further away from the mainland (Ricklefs 2007). Very often, colonizing species immigrated to the islands from source pools with limited number of species and the spatial dynamics of this type are unidirectional (Holt 1996). This means that, in many cases, in oceanic islands and in many isolated habitat patches, once a community was established by colonizing species, its further immigration is insignificant compared to on island that is less isolated (Brown and Kodric-Brown 1977, cited in Holt 1996). In island theory, the determinant factors for the spread of species from one region to another are the island area, distance, spatial configuration of the main source and eventual stepping stones – intermediate island between the main source and the recipient island (McArthur and Wilson 1967). The theory focuses on the species at the same trophic level which are not interacting although there may be a competition among them.

According to Holt (1996), food webs on islands are simpler because of the lower number of species and the length of food chain depends on the islands area. This notion is also supported by MacArthur and Wilson (1967) who hypothesized that the species – area relationship in which case the number of species occupancy increases with the area, A, of island and habitat patch is described by species–area relationship. This relation fits a power function, $S = cA^z$, or $\log(S) = \log(c) + z\log(A)$, where c and z are constant values fitted to the data; c is a parameter that depends on taxon and biogeographic region most strongly on population density as determined by these parameters, and z is a parameter that changes little within or between taxa in different parts of the world. The value of z is between 0.15 and 0.45.

Metapopulation Dynamics

Human land-use has caused fragmentation of natural landscapes throughout the world (Whitmore 1997). Habitat patches and edges of different size and shape that differ in habitat quality are the end output of the fragmentation process in the landscape. Consequently, isolation and formation of metapopulations is presently a common phenomenon in heterogeneous landscapes at different spatial scales. The term metapopulation was introduced by Levin (1970, cited in Farina 1998) to describe a population of populations that actively move among each other. Metapopulations are systems in which there are fluxes of individuals from time to time between subpopulations (Farina 1998).

Metapopulation theory (Levin 1969, 1970) describes a network of patches, some occupied and some not, where subpopulations are interacting (“winking”). The model is then based upon presence-absence, not a demographic model like source-sink dynamics. In fragmented and heterogeneous landscapes, in most cases species are patchily distributed across space. In a metapopulation, there is a genetic or demographic connection between the subpopulations otherwise they are considered as separated populations. The metapopulation theory is related to island biogeography (MacArthur and Wilson 1967) with fundamental processes of extinction and colonization.

The concept of metapopulation theory has been used as an ecological tool for understanding the population or species dynamics in fragmented habitats including the crop pests and natural enemies’ population in agricultural landscape. Populations living in a heterogeneous area may be isolated from each other because of less favorable habitats matrix and interact through emigration or immigration processes. The local extinction of the isolated subpopulation then gradually will happen (Farina 1998). When the individuals migrate to an empty habitat patch, a new subpopulation will be formed. On the other hand, if there is no movement between patch habitats, the subpopulations are isolated from each other and if they are small in size, they face high risk of extinction and thereby the total population slowly goes extinct (Ricklefs 2007). However, the size of the habitat patches often varies and, in contrast to small patches, larger patches could support larger subpopulations than small sized patches. Therefore, subpopulations supported by larger patches have low risk of extinction when compared to subpopulation in small patches. For example, as mentioned by Ricklefs (2007), the effect of patch size was shown on two systems of islands in Finland. These islands are situated in two lakes, and vary in size from 0.1 to 1000 ha. In terms of distance, these islands are located at 0.1 to more than 2 km from other islands. On these islands, the distribution of the shrew (*Sorex araneus*) was observed and larger islands (>1 ha) had greater shrew populations than smaller islands. In plants, according to Silvertown and Charlesworth (2001), even though it is difficult to find clear examples of metapopulations, the local population dynamics is achieved by seed dispersal between populations rather than from seed bank and if these are not synchronized, local extinction of the population will take place. Therefore, seed dispersal has profound importance for the distribution and persistence of subpopulations of plants in fragmented landscapes.

Landscape Heterogeneity

Landscape refers to an area that is spatially heterogeneous caused by different factors of interest (Turner 2001). There are several types of landscapes we observe on earth; agricultural, urban, lowland and mountainous landscapes, natural and developed landscapes are some to be mentioned. The pattern or spatial configuration of agricultural landscape may consist of patches of native forests with different size and shape, forest edges, narrow forests along streams, scattered wild trees of different cover values, tree plantations, and coffees under the forest patches, crop lands, landforms of different settings and villages. Some elements of a landscape could be described from the photo shown in Fig. 2 from southwest Ethiopia. The rapid changes in patterns of the landscape have caused ecologists to assess the impacts of the changes on spatial and temporal basis.



Figure 2. Example of agricultural landscape (Photo by Debissa Lemessa 2010).

The term *landscape ecology* was coined by the German biogeographer Troll (1939, cited in Turner 2001), from the root of the European traditions of regional geography and vegetation science. Thereafter, the formation of the European Landscape Convention (Council of Europe 2003, cited in Ode et al. 2010) has increased the importance of landscape issues in planning and policies throughout Europe. Therefore, landscape ecology refers to the interaction between spatial pattern and ecological process emphasizing the causes and consequences of spatial heterogeneity across a range of scales, spatial and temporal dimension of processes (Turner 2001). Specifically it focuses on the development and dynamics of spatial and temporal heterogeneity (such as dissimilar elements: mixed habitats and cover types in a landscape) within and across landscape and its impacts on biotic and abiotic (climate, topography, and soils) processes. Heterogeneity stands for the spatial complexity of the mosaics in landscape.

Features of Landscape Heterogeneities

According to Farina (1998), there are at least three types of heterogeneity that could be taken in to account in landscape ecology.

1. Spatial Heterogeneity

Spatial heterogeneity is a pattern that affects several ecological processes, such as soil formation, weathering, plant and animal distribution, abundance and movements, water and nutrient fluxes, energy storing and recycling etc. Spatial heterogeneity may be categorized in to **Horizontal** and **Vertical** heterogeneity. Horizontal heterogeneity refers to the irregular distribution of land cover naturally and because of human disturbance regimes, for instance, due to diverse cultivations in the landscape. Conversely, vertical heterogeneity represents vertically uneven distribution of vegetation above ground.

2. Temporal Heterogeneity

Temporal heterogeneity is similar to spatial heterogeneity but here the variation is measured at a certain point in space along the time series. Although two locations may have identical patterns, the heterogeneity will emerge at a certain point in time.

3. Functional Heterogeneity

Functional heterogeneity is the variation in ecological entities, such as the pollination, predator-prey interaction and fluxes of nutrients and energy (Pickett and Cadenasso 1995). The functional heterogeneity might influence the distribution of individuals, populations, species, and communities in landscapes. In general, heterogeneity could cause the formation of borders, edges and contrasts between patches in landscapes.

Role of Matrix in island biogeography and metapopulation theories

A population is a group of individuals of a particular species within a given area. Naturally, each population occupies patches of suitable habitat. Natural habitats also exist as mosaic of different habitat patches in natural landscape. Currently, uniform and homogenous habitats on vast areas will not exist (Ricklefs 2007). In landscape models, habitat matrix is the type of habitat surrounding suitable habitat patches through which individuals of a particular species move to colonize the other alternative patches in the landscape. The theory of island biogeography was not apparently stated for continental landmass or landscape. As described in the section of landscape heterogeneity, landscape comprises of habitat matrices, isolated patches of different shapes, edges and distances, corridors that connects patches. Terrestrial habitats are not as sharply isolated as marine islands and the composition of the landscape differ in many aspects. Hence, patches colonization and extinction pattern of species in heterogeneous landscapes may be beyond the theory of oceanic island biogeography.

The existence of matrices, different quality of food sources, variation in microclimates, and higher diversity of species with different dispersal or movement rate in the landscape make different from the theory of the island biogeography which mainly focuses on colonization-extinction as governing factors for the number of species to reach steady state in habitat patch.

Cook et al. (2002) also reported that the island theory predictions fit well to the diversity patterns if only the species in the matrices are removed from the patch samples in habitat fragments of landscape. On top of this, Perfecto and Vandermeer (2002) pointed out that species survive in matrix habitats. Moreover, colonization and dispersal through the matrices might also be different from that of colonization of species on islands (Tschirntke and Brandl 2004) and the characteristics of habitat matrix should be incorporated in colonization-extinction dynamics in fragmented landscapes (Brotons et al. 2003). On the other hand, fundamentally, the theory of metapopulation is related to the theory of island biogeography. The landscape model may also go beyond metapopulation model as single species population dynamics might not describe or predict the dynamics of populations in reality in the fragmented or heterogeneous landscape. This is because a landscape model considers the effects of differences in habitat quality within the matrices and patches. The actual movements of individuals of different species between patches depend on the surrounding landscape and habitats found along the way (Ricklefs 2007). Moreover, the habitat matrix also influences the movement of individuals from one subpopulation to another. For example, in heterogeneous agricultural landscape, the natural enemies may avoid interference by moving to plant subpopulations or crops not occupied by their competitors (Onzo et al. 2003) and when the predators occupy different niches they complement each other within a crop field.

Agricultural Landscape

Spatial patterns of crops (both perennial and annual) cultivated in agricultural landscapes throughout the world vary from place to place. Habitat loss due to agricultural intensification is a primary cause of landscape change (Tilman et al. 2001). According to Saunders et al. (1993), habitat loss at the landscape scale, in regions where modern agriculture is practiced, has often reached 80% or greater. In this connection, Tilman et al. (2001) predicted that if this trend continued, 10^9 hectares of natural habitat would be converted to agriculture by 2050. On top of this, the increasing use of pesticide is also at the expense of the conservation of biological control. The heterogeneity of agricultural landscape at different spatial scales may influence the pest population differently and their impact on crops also varies accordingly for they move between crop fields and wild habitats. Thus, it is a challenge for agroecologists to identify the diversity or level of heterogeneity either at local (small) or regional level that will

achieve desirable result in crop yield regulating the pest population below economic threshold level (Altieri 1991c).

Top-down regulation of crop pests

Natural regulation of pest population is being exerted by naturally occurring predators and parasites (and diseases) in the local agroecosystem sharing the same habitat and belonging to the same ecological community. This population regulation is sometimes referred to as the *balance of nature* or *natural control*. The control of pest populations in crop production by either conserving or inducing natural enemies could have both environmental and economic benefits compared to chemical pesticide use (Östman et al. 2003). Different results were reported regarding the natural regulation of pest population; for example, Finke and Denno (2004) reported that a simplified natural enemy community controls pest populations either equal to or better than a complex of natural enemies due to the antagonistic interaction or intraguild predation, the consumption of one predator by another predator while competing on the same prey (Straub et al. (2008). However, Cardinale et al. (2003) and Schmidt et al. (2003) reported that pest population regulation efficiency of natural enemies increases as their diversity increases in the crop field. In this case, the complementarity of niches (determined by different microclimate like temperature and humidity) among the diversity of natural enemies may enhance the pest population regulation efficiency.

Furthermore, Tscharrntke et al. (2007) reported that the structure and heterogeneity of agricultural landscape influences natural pest regulation because of the availability of alternate hosts/prey and food for predators and parasitoids in the landscape. Moreover, structural complexity of the landscape reduces pest incidence due to impediment of herbivore movement and colonization in diverse plant communities. Thus, it is essential to understand the inter-relationships and dynamics between natural enemies and pests on a landscape context at different levels (Thies et al. 2003). On the other hand, simple monocultures or homogeneous plant communities are concentrated resources in time and space and create conducive environments for the buildup of the herbivore or pest populations. In any case, populations of crop pests can be suppressed by the natural enemies in agroecosystems (Denno and Lewis 2009). Costamagna and Lands (2006) has reported that top-down processes control pest populations in crop fields significantly.

For the sake of illustrating how top-down control could work a specific example of the trophic interaction found among tigers or leopards, baboons and crops (e.g. maize) could be taken. Accordingly, tigers or leopards feed on mammal pests (e.g. baboons), consequently, the population of baboons will be suppressed and the crop biomass (e.g. maize) will be released. Another example could be invertebrate natural enemies such as spiders, lady bird beetles and wasps that eat and parasitize insect crop pests (e.g. lepidopterous moths, stem borers) and so limit the pest population. It is from this reality that the biological control method has been used as an integrated pest management in agricultural crops.

In this regard, Caltagirone and Doult (1989) reported an example of the accidental introduction of Cottony cushion scale (*Icerya purchasi*) from Australia to California. As a result, the California citrus industry was heavily damaged by this pest. To alleviate this problem a predator, ladybug beetle (*Rodolia cardinalis*) was collected from Australia and released to this citrus farm and after a short time it controlled the scale insect and saved the citrus farm. The basic interactions in nature form consumer–resource chains, which build up biological communities in different trophic levels. Predator–prey, herbivore–plant, and parasite–host relationships either increase or decrease the population size of prey. Predators (for example, birds) consume individuals from a prey population (for example, insect pests), insect pests attack plants; including crops, and parasitoids consume the living tissues of these insect pests. These prey population might be regulated from above by predation and from below by production. When higher trophic levels, for example birds feed on insect pests and determine the size of the pest population the situation is a top–down regulation process. Conversely, when the size of the prey population, for example an insect pest, is determined by the availability of its food, the condition is a bottom–up control mechanism (Ricklefs 2007). However, the strength of these processes varies in space and time (Stiling and Moon 2005) as a result of habitat loss and isolation, which weakens top-down control (Terborgh et al. 2001).

The antagonistic interaction among predators may lower the strength of top-down regulation of prey populations (Rosenheim et al. 1995). However, the impact of intraguild predation of herbivore populations might vary as a result of bottom-up factors such as habitat quality (Forkner and Hunter 2000), vegetation structure and complexity and behavioral differences (Finke and Denno 2002) For example, in complex-structured vegetation, the intraguild predation (e.g. between mirid bugs and wolf spiders) is low since complex vegetation could be a refuge for intermediate prey (e.g. mirids) than simple habitats. As a result, due to this

antagonistic interaction, the population of planthoppers will be released in complex habitats (Finke and Denno 2002).

Natural enemies in habitat interfaces

Natural pest control is an important ecological service or function that often depends on the spillover of natural enemies from natural habitats to crop fields. Several reports indicate that agricultural landscapes with low amount of natural habitat generally support a low diversity of natural enemies which results in lower predation or parasitism regulation of pest populations compared to landscapes with a high proportion of natural and undisturbed habitats (Roland and Taylor 1997). The diversity of the agricultural landscape mosaic, characterized by the variety of crops and wild plants, and their spatial arrangement (for example, the size of fields and the heterogeneity of their spatial distribution) affects the abundance, diversity, and dispersion of pest species and their populations. In other words, the adjacent habitat like vegetation and their size, shape and spatial pattern influence the population of pests and insects in general (Fry 1995). Thies et al. (2003, 2005) revealed that parasitoid diversity and parasitism rates are also higher in structurally complex landscapes composed of arable fields and non crop habitat than in simple landscapes of only arable fields. Undisturbed or perennial non crop habitats such as field margins, fallows, hedgerows, and woody vegetation in agricultural landscapes can supply parasitoids with alternative hosts and sources of food (i.e., pollen and nectar). The availability of alternative sources of food increases parasitoid longevity, fecundity, population size, and spread to surrounding crops (Lee et al. 2004).

A diversified agricultural landscape mosaic may sustain a broader diversity of natural enemies, where the abundance, diversity or potential impact of insect natural enemies increases with increasing diversity of non-cultivated habitat in the landscapes surrounding crop fields. According to Elliott et al. (1999; 2002a, b), this holds true for generalist predatory insects such as coccinellid beetles, and for the specialized parasitoids (Rand et al. 2006). However, the species diversity and abundance of predators may be influenced by several other factors like the types or species of crops grown adjacent to each other and to the natural habitats. In this regard, the result of the finding of Altieri and Todd (1981) indicated that predators are more abundant at the edges of soybean fields adjacent to pea fields and weedy tracts than in soybean edges adjacent to vegetation-free fields. In heterogeneous landscapes

the level of provision of resources by different habitat types to natural enemies varies and this may affect their abundance and diversity and the efficacy of natural pest control as well (Wyckhuys and O'neil 2007). Therefore, the presence of trees in agricultural crop fields may increase or reduce pest density since it modifies the microclimate in the intercropped area because of its shade effect which induces change of temperature and moisture in understory intercrops. According to Kruess (2003), Ndemah et al. (2007) and Matama-Kauma et al. (2008) the density or abundance of parasitoids and stem borer is higher in cultivated habitat and lower in natural habitat and conversely their diversity is higher in natural habitat than in cultivated areas. In addition, the finding of Mailafiya et al. (2010) indicated that the natural habitats are the refugia for the diversity of the parasitoids. However, Guharay et al. (2000) found in their study of the effect of shade on insect pest in coffee field that the damage by leaf miner (*Leucoptera meyricki*) was reduced by shade, whereas the coffee berry borer (*Hypothenemus hampei*) increased under shade. Hence, the effect of landscape fragmentation on the diversity of parasitoids and pests needs further research. Under agroecosystems where extensive monoculture crop growing is taking place, a pest population explosion may be induced and sometimes a proportional increase of natural enemies will occur. Thereby the natural mortality rates for the pest remain high and the final pest population will be reduced.

The rate of growth of parasitoid populations is usually too long in agroecosystem to reach community stability and to be effective in pest population control. As a result, in annual crops such as pulses, cereals and vegetable, parasitoids will not get sufficient time to build up their population to a level where they can exert controlling effect. In such cases, non-specific (polyphagous) predators and parasitoids may be more important in regulating the pest populations (Hill 2008). Alternatively, vertebrates like birds, mammals and invertebrate predators and parasitoids reduce populations of pests through either direct feeding on the individuals or indirectly competing for the shared food resources (Gomez and González-Megias 2007). Some bird species, for instance, might feed either on larva of crop pests (e.g. larva of system borers) or compete with stem borers feeding on seeds of maize or sorghum in the field. In general, natural control of pest populations is the result of trophic interactions among organisms like prey-predator, and host-parasitic relationships although land-use (e.g. change of natural habitat to agricultural land) affect such interactions (Altieri and Nicholls 2000).

Factors affecting the fluxes of natural enemies in agricultural landscape

Very often, resources availability varies in agricultural habitat. Cropping systems are also season dependent. Hence, the relative availability of resources in crop fields and natural habitats will in most cases vary through time and this determines the magnitude and direction of the spillover of predators. In this regard, Rand et al. (2006) described the movement of natural enemies between natural habitat and crop fields; when crops are growing natural enemies spillover to crop fields and move back to the wild habitat when the crops are harvested. Here, predators initially colonize the crop fields from adjacent natural habitats and then their population will build up within the landscape during the growing season while feeding on crop herbivores (pests). In the late season the resource quality declines within the crop fields when crops are harvested which results in predator emigration and concentration within remaining natural habitats in the landscape. Consequently, the population of the pests dramatically decreases. This indicates that the spatiotemporal dynamics in agricultural landscape matrix play a great role in determining the magnitude and direction of cross-edge spillover of the natural enemies and pest populations. For example, Thorbek and Bilde (2004) and Hogg and Daane (2010) found that generalist predators like spiders, carabid and staphylinid beetles responded to a variety of crop management practices primarily by emigrating which in turn resulted in an aggregation of predators in less disturbed habitats. This situation is happening when there are temporally shifting resources in the agricultural landscape based on season. Where there are complementary resources (from natural and crop habitats) the population growth rate of the predators will increase and aggregation will occur at the edges where it is possible to access both resources (Rand et al. 2006). Landis et al. (2000) and Tylianakis et al. (2004) further stated that ‘Natural or semi-natural habitats may provide over-wintering sites, alternative host species, or alternative energy sources that are critical to sustaining enemy populations. Furthermore, Bianchi and van der Werf (2003) depicted that landscapes that are rich in non-crop habitats have extended crop and non-crop interfaces which enhance early season field colonization by natural enemies. Many nectar-feeding natural enemies such as parasitoids, syrphids and chrysopids are also more abundant near field edges than in field centers (Nicholls et al. 2001; Tylianakis et al. 2004). Landis et al. (2000), from agroecosystem studies, suggested in general that natural habitats can be important sources of natural enemies colonizing crop fields, and proximity to such habitats may result in increased control of agricultural pests. To sum up, the following factors may

determine the fluxes of natural enemies in agricultural landscape; (1). size of the crop field, (2) number of available alternate habitats, (3) quality of alternate habitats and (4) distance to alternate habitats.

Crop pest Regulation Pertinent to Tropical Landscapes and Challenges

High rates of leaf production and litter fall have favored insect herbivory in the tropics (Turner 2001), but increased deforestation rate in the tropics has resulted in isolated fragments of forest patches of various sizes and shapes surrounded by a non-forested matrix (Turner 1996). This modification in the landscape causes a reduction in forest area and the creation of abrupt edges between forest and non-forest habitats, affecting the predators, parasitoids, seed dispersers, pollinators, and others like decomposers.

Relative to the temperate regions little is known in the tropics about the consequence of landscape modifications on the ecological functions at different spatial scales (Benítez-Malvido and Lemus-Albor 2005). Furthermore, it is also pointed out by Faveri et al. (2008), that how the changes caused by habitat fragmentation affect the interaction between herbivores and their host plants, as well as between herbivores and their natural enemies is not well understood or was little studied in the tropical regions (Benítez-Malvido and Lemus-Albor 2005).

There are different views and suggestions reported from different researchers. Some authors suggest that fragmentation can negatively affect the abundance and diversity of insect predators and parasitoids (Kruess and Tscharntke 1994), and this favors populations of insect herbivores. Others propose that the amount and quality of food resources for herbivores may also change with habitat fragmentation because light levels increase near fragment edges, and light can affect plant productivity and leaf chemistry (Yamasaki and Kikuzawa 2003) and accordingly this negatively affects the insect herbivores or crop pests. This shows the importance of further research mainly on the top-down and bottom-up regulation of the pest population sizes in fragmented landscapes of the tropical regions, though, it is a challenge to understand how the natural pest control is affected by agricultural or land use practices in agroecosystems (Wilby et al. 2006).

In general, this is a big challenge to understand the ecological processes in the tropical and subtropical regions during which the rate of deforestation and fragmentation of landscape is outstripping the resilient potential of the wild habitats mainly as a result of intensification of

agriculture. Furthermore, today, as a result of modern agriculture, monoculture is intensively practiced all over the world with the application of agrochemicals (artificial fertilizers and various pesticides) to boost crop production breaking or overriding the ecology-farming linkages. However, according to Altieri and Nicholls (2004) the pest problems were not mitigated and are rather on increasing pace.

Conclusion and future directions

A landscape is a heterogeneous area that constitutes spatial patterns and configurations of various elements such as forest patches, scattered trees, corridors, forest edges and crop fields. However, human land-use or intensification of agriculture has caused the fragmentation of natural landscape. As a result, it is now common to observe the fragmented landscapes that considerably vary spatially and that change on temporal basis throughout the world. Consequently, the disruption of the ecological functions like trophic interactions, formation of the metapopulations, migration and extinction of species because of isolation as in the case of the island biogeography are some of the outputs of the fragmentation at different spatial scales. The theories of island biogeography and metapopulation may not fit to the present landscape model because of the rapid changes in landscapes as a result of fragmentation processes. These ecological complications are big challenges to understand, for example, the top-down and bottom-up processes, natural pest regulation dynamics in agricultural landscape in relation to the spatial heterogeneity of wild trees and forests. These are profoundly the challenge in the tropical regions where presently the rate of degradation of biodiversity and fragmentation is rapidly taking place and where information is lacking regarding the dynamics of crop pests and the natural enemies in the landscape. Hence, from the present review, further research was suggested in the tropical region according to its local and regional conditions.

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