

Biodiversity Conservation in Tropical Agroecosystems

A New Conservation Paradigm

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It is almost certainly the case that many populations have always existed as metapopulations, leading to the conclusion that local extinctions are common and normally balanced by migrations. This conclusion has major consequences for biodiversity conservation in fragmented tropical forests and the agricultural matrices in which they are embedded. Here we make the argument that the conservation paradigm that focuses on setting aside pristine forests while ignoring the agricultural landscape is a failed strategy in light of what is now conventional wisdom in ecology. Given the fragmented nature of most tropical ecosystems, agricultural landscapes should be an essential component of any conservation strategy. We review the literature on biodiversity in tropical agricultural landscapes and present evidence that many tropical agricultural systems have high levels of biodiversity (planned and associated). These systems represent, not only habitat for biodiversity, but also a high-quality matrix that permits the movement of forest organisms among patches of natural vegetation. We review a variety of agroecosystem types and conclude that diverse, low-input systems using agroecological principles are probably the best option for a high-quality matrix. Such systems are most likely to be constructed by small farmers with land titles, who, in turn, are normally the consequence of grassroots social movements. Therefore, the new conservation paradigm should incorporate a landscape approach in which small farmers, through their social organizations, work with conservationists to create a landscape matrix dominated by productive agroecological systems that facilitate interpatch migration while promoting a sustainable and dignified livelihood for rural communities.

Key words: agroforestry; polycultures; agricultural intensification; land sparing; biodiversity-friendly agriculture; metapopulation theory; fragmentation; agricultural landscapes; agricultural matrix; social movements; social justice

The Tropics and the Charismatic

The tropics have been a sort of Holy Grail for ecologists. The famous latitudinal gradient of species diversity shows a dramatic increase in species diversity for almost all organisms. Explaining this amazing fact has occupied the

creative energies of ecologists since Merian's famous drawings of Surinamese insects fired the imagination of Dutch naturalists well before the Victorian English captured the historical initiative. In modern times the debate continues with many hypotheses contending for center stage. For example, Palmer (1994) listed no fewer than 21 hypotheses culled from the literature, and certainly, the list has grown since that time.

Whatever the debates about the latitudinal trend, there is little doubt that tropical areas

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of the world contain the vast majority of terrestrial biodiversity and thus merit considerable attention by those concerned with conservation. Consequently, devising action plans for stemming the tide of biodiversity loss most properly has been focused on tropical areas of the world. Although most ecologists concerned with biodiversity conservation would agree with this focus, there are two points of disagreement, at least in practice, if not actually articulated very clearly in the literature. The first has to do with the tendency we seem to have to focus on large charismatic megafauna, such as elephants and jaguars. Although one may argue that this is a good political strategy (Leader-Williams & Dublin 2000), most of the biodiversity, and arguably the most important for ecosystem function (Wilson 1987; but see also Terborgh 1988), is not found within these large charismatic organisms. Of the more than million species of eukaryotic organisms formally recognized, vertebrate animals represent a very small fraction (there are 10 times as many plant and at least 100 times as many invertebrate species). Furthermore, the attention of the research community is actually in reverse proportion to the abundance of organisms (e.g., between 1987 and 2001, 70% of the papers in the two leading conservation biology journals were focused on vertebrates and only 10% on invertebrates [May 2007]).

The second point of disagreement has to do with what might be called “charismatic habitats.” There seems to be a certain romantic attachment to the idea of “pristine” environments, no matter how much the historical and anthropological literature suggests there are very few of them. Likely a byproduct of European bias, the neo-Victorians sometimes confuse biodiversity conservation with their romantic vision of pristine edens. Consequently, modern *Homo sapiens*, like the Pleistocene hunters before us, remains the enemy of biodiversity and anything that our species does is regarded as suspect at best. Sometimes coupled with neo-Malthusianism (also

inherited from the Victorians [Davis 2001]), the conservation community is highly suspect in many quarters of the world, most specifically among the world’s poor, the majority of whom share the globe with the mega hotspot of biodiversity.

The romanticism of the pristine also affects our ability to see clearly the role of agriculture in biodiversity conservation. On the one hand, there is a diverse literature demonstrating the high levels of biodiversity contained in particular types of agroecosystems (Pimentel *et al.* 1992; Perfecto *et al.* 1996; Collins & Qualset 1998; McNeely & Scherr 2003; Götz & Harvey 2007). On the other hand the importance of agroecosystems at the larger landscape level can no longer be ignored, given the theoretical and empirical literature on metapopulations and the agricultural matrix (Vandermeer & Carvajal 2001; Perfecto & Vandermeer 2002; Jules & Shahani 2003; Baum *et al.* 2004; Banks 2004; Manning *et al.* 2004; Antongionanni & Metzger 2005; Berry *et al.* 2005; Harvey *et al.* 2005; Koelle & Vandermeer 2005; Tscharnke *et al.* 2005; Vandermeer & Perfecto 2007; Vaughan *et al.* 2007). Yet the dichotomous view of preserved land for biodiversity versus agricultural land for economic development, with significant tradeoffs between them, remains influential in the conservation and development literature (Lee & Barrett 2001; Mellor 2002; Terborgh *et al.* 2002; Green *et al.* 2005).

In this article we first provide a historical narrative about agricultural development in the tropics to set the stage for our argument. We then discuss the ecological theory as it pertains to how biodiversity is maintained in fragmented landscapes. Then we examine the concept of agricultural intensification and its impact on biodiversity and review the literature on biodiversity in several types of tropical agroecosystems. Finally, we bring these lines of thought together into what we regard as a new paradigm of biodiversity conservation, one that combines popular movements for social justice with sustainable agriculture to focus conservation concerns at a large landscape level.

Historical Overview: Agriculture and International Politics

Tropical lands have been occupied by hominoids for at least 10 million years, by hominoids that knew how to use fire for at least a million years, and by *Homo sapiens* who knew and practice agriculture for five to ten thousand years (Harlan 1971; Piperno & Pearsall 1998). The vast majority of that time agricultural people had little effect on tropical biodiversity. A significant change in the biodiversity/agriculture relationship in the tropics was ushered in by European and U.S. colonialism and imperialism (although Chinese and Indian expansion on their immense land masses, were arguably significant earlier [Grove 1995; Tucker 2000; Elvin 2004]). A combination of logging and plantation agriculture converted enormous tracts of natural habitat into agriculture and pastures to feed the European and North American markets for wood, sugar, tea, coffee, meat, and later bananas and other tropical fruits (Tucker 2000; Topik *et al.* 2006). The remnants of these 17th and 18th century systems of extensive production for colonial and neocolonial markets remain a particularly important element of agroecosystems in the tropics, especially with respect to their impact on biodiversity (Tucker 2000; Donald 2004). Yet the bulk of rural people (still a majority in the tropics, although declining as a percentage) rely on small-scale agriculture for their sustenance.

Traditionally the small tropical farmer engages in what might be called “natural systems” agriculture, with cues from the natural environment combining with oral traditions in constantly evolving practices (Gliessman 1992; Gómez-Pompa & Kaus 1992; Altieri 2004). Thus, for example, on most oxisols and ultisols in high-rainfall areas of the Americas and Asia, trees are an integral part of the agroecosystem, much as they form the key physical feature of the local natural environment (Michon *et al.* 1983; Ewel 1986; Sánchez & Benítez 1987; National Research Council 1993; Miller & Nair 2006). Coffee and

cacao had long been produced under the shade of trees in Mesoamerica and South America, such that traditional coffee and cacao farms are indistinguishable from native forest from a satellite (Perfecto *et al.* 1996; Moguel & Toledo 1999; Rice & Greenberg 2000; Götz & Harvey 2007). Many other examples could be cited (Vandermeer 2003).

Agricultural landscapes in the tropics were thus characterized by historical remnants of: first, large and extensive plantations inherited from colonial times, sometimes radically altering the natural ecosystems, sometimes seemingly imitating them, but always extensive in area; and second, a smaller overall area in which many more people engage in semisubsistence activities, sometimes articulating with markets, sometimes not. Subsequently, after World War II, a major new agricultural intensification trend, imported from the developed countries, began penetrating this landscape of historical legacy (Hayami & Ruttan 1985; Olmstead & Rhode 1993; Magdoff *et al.* 2000). Complemented by the Green Revolution (i.e., high-yielding varieties, agrochemicals, and other agricultural technologies), this agricultural intensification program increased productivity but at a high environmental cost (Matson *et al.* 1997; Tilman *et al.* 2001a; Tilman *et al.* 2002), including the loss of biodiversity (Perfecto *et al.* 1996; Giller *et al.* 1997; Krebs *et al.* 1999; Tilman 1999; Wilby & Thomas 2002; Tscharntke *et al.* 2005).

The tropical landscapes of today are consequently characterized by a mosaic of large plantation-type agriculture (some of it intensive and some extensive, including pastures) interspersed with medium and small farms and forest fragments. In this type of landscape where the natural habitats are highly fragmented and embedded in an agricultural matrix, it is imperative to base conservation practice on solid ecological theory and, as we shall argue, to recruit the participation of farmers, in particular farmers' organizations and rural-based social movements, as an integral part of those plans.

Ecological Theory for Fragmented Landscapes

From the long history of life on Earth, there is little doubt that species go extinct on a regular basis—that is one of the main patterns of biodiversity. What is less evident is that some species regularly disappear locally. Most of the time, such local extinctions are temporary, a consequence of migrations from other regions or other patches of habitat (Hanski 1999). While paleontologists provide great insight into the extinction process at geological time scales, the ecological question of just what determines whether a local extinction will occur or not has been foremost on the agenda of ecologists.

In trying to understand patterns of biodiversity over time, ecologists and paleontologists have emphasized the two balancing processes of extinction—the disappearance of species—and speciation—the evolution of new species. However, when focusing on the patterns of diversity in contemporary time, whether latitudinal/altitudinal patterns, island patterns, or patterns associated with land use and agricultural intensification, ecologists have focused more on the processes that result in extinction. Since an area with a high extinction rate is expected to have lower biodiversity than an area with a low extinction rate, understanding the process of extinction (or its avoidance) gets us closer to understanding patterns of biodiversity.

Populations have complex distributions in space. Studying a population of butterflies on the Åland Islands in Finland, Hanski (1999) showed that although each individual habitat patch is incapable of maintaining a population of these butterflies, the population persists due to its metapopulation structure. The mechanism that makes this possible is migration among the habitat patches. While at any time there is a certain likelihood that the population of a given patch will go extinct locally, there is also a likelihood that migrants from some other patch will arrive. In other words, if the rate of local extinction (i.e., the probability

that a given subpopulation will go extinct in some period of time) is smaller than the rate of migration (i.e., the probability that another individual will arrive at that habitat patch before all of the subpopulations go extinct), the overall population, or the collection of all the subpopulations that live on all those islands, will persist over the long term.

The fundamental equation of metapopulation biology is deceptively simple, $p^* = 1 - e/m$, where p^* is the equilibrium fraction of habitats that are occupied by a species, e is the extinction rate and m is the migration rate (Levins 1969). If the extinction rate is small, p^* is large. If the migration rate is small, p^* is small. If the migration rate decreases to the point that it approaches the value of the extinction rate, the population will go extinct. While this simple equation may be too general for planning conservation strategies for particular landscapes, it nevertheless is useful as a qualitative tool for evaluating various propositions for conservation in fragmented landscapes.

The Nature of Extinction Processes

It is almost certainly the case that many populations in nature have always existed as metapopulations at some scale. But in the contemporary world the idea has become more important than ever due to fragmentation. The world has, for all practical purposes, been divided up into a patchwork of habitats (Gascon *et al.* 2000), and almost the entire terrestrial surface of the globe is a mosaic of different kinds of habitats. There is now a considerable literature concerning the nature of the local extinctions that are normally expected to occur in metapopulation contexts. In the end, each fragment does not have to provide all the necessities to maintain a population in perpetuity, but exists in the context of other fragments that provide propagules for species that have gone locally extinct because the fragment was too small to maintain a population over the long term (Hanski 1999).

Metapopulation studies in general have led ecologists to realize that local extinctions are common and natural (Newmark 1995; Foufopoulos & Ives 1999; Ferraz *et al.* 2003; Werner *et al.* 2007). For example, in an examination of historical changes in the mammal fauna of North American national parks, Newmark (1995) reported a surprisingly large number of extinctions, even in relatively large parks. Foufopoulos and Ives (1999) gathered data that convincingly demonstrated that the patterns of reptiles on islands in the Aegean Sea were a consequence of extinction events during the past 10,000 years. Werner and colleagues (2007) documented a high number of local extinctions of amphibians that had been surveyed 20 years earlier, but also noted that the extinctions were balanced by new migrations. An important recent result is that of Ferraz and colleagues (2003) from long-term experiments on forest fragmentation in Amazonia. While smaller patches of forest have higher avian extinction rates than larger ones, the actual extinction rates of even the largest patches are surprisingly high. Indeed, some are so high as to suggest that the only acceptable size for a biological preserve is one that is far beyond reasonable expectation under current political circumstances (Ferraz *et al.* 2003). These and many other studies leave no doubt that extinction at a local level is a normal process and is not a process that we could stop. This conclusion has major consequences for the conservation of biodiversity in the highly fragmented forests of the humid tropics and the agricultural matrix in which they are embedded (Vandermeer & Perfecto 2007).

Recent theoretical studies suggest that for some organisms the spatial extent necessary for their preservation may be unusually large, far beyond what any current or imagined future political arrangement might tolerate, or even what may be available in natural/unmanaged habitat. As an example, Hubbell (2001) postulates that recruitment limitation, or failure to disperse to suitable habitat patches, is one key factor in maintaining tropical tree di-

versity. Long-distance dispersal events, under Hubbell's formulation, are important in maintaining species diversity. Therefore, fragmenting the forest and consequently limiting the rare dispersal event from point *x* to point *y* in the original spatially extended forest is likely to cause an imbalance between the inevitable local extinctions and what used to be dispersal, now limited through fragmentation. The result would be expected to be a concomitant reduction in regional biodiversity, as observed, at least in the examples cited above (Newmark 1995; Foufopoulos & Ives 1999; Ferraz *et al.* 2003; Werner *et al.* 2007). Unfortunately, such expected regional and global extinctions are likely to occur far into the future, making the political case for biodiversity conservation here and now very difficult.

The Matrix Matters

Some habitats harbor great biodiversity, others less. But those habitats that harbor less biodiversity may be extremely important for those that harbor more. Indeed, in the fragmented landscapes that characterize almost all of the world's terrestrial surface, those habitats that are biodiversity "poor," may be extremely important as passageways for the habitats that are biodiversity "rich." The matrix within which the "good" habitats are located may be of various qualities in terms of its ability to support necessary services for those "good" habitats. In short, a collection of biological reserves in a sea of intensive agriculture dominated by monocultures and pesticide applications is probably far worse for overall biodiversity conservation than a smaller collection of biological reserves in a sea of diverse agroecosystems managed organically and with some tree cover. The matrix matters!

Focusing on the quality of the matrix is similar to, but different in important ways from, the focus on corridors, an idea that was popular in conservation biology for some years (Rosenberg *et al.* 1997; Anderson & Jenkins 2005). The idea was that patches of natural habitat needed

to be connected with one another, for reasons similar to the reasons subpopulations need to be connected in a metapopulation context. A corridor, in its original formulation, was a thin strip of natural habitat that connected these patches of habitat (Rosenberg *et al.* 1997). The whole point was to make sure that there was communication among patches or among individuals in the populations, or at least the potential for exchanging genes among populations. There was something of a flourish of interest in corridors about 10 years ago, but interest has subsided. Most studies concluded that the idea did not work well, for a variety of reasons that tended to be specific to the region or organisms under consideration (Beier & Noss 1998).

However, many of the same goals sought by conservation biologists with corridors are realizable in the context of the matrix. The idea is to maintain or construct a matrix that is “biodiversity friendly” at least in the sense that it facilitates interpatch migration. For example, a shaded cacao plantation may not allow for the persistence of a particular orchid species, but it may provide a habitat that will allow the movement of pollinating euglossine bees, effectively facilitating the mixing of genes between patches of appropriate habitat. Likewise, scattered trees in a pasture may facilitate gene flow of trees between subpopulations in a fragmented habitat (White *et al.* 2002). Similarly, a specialist forest ant species may not be able to establish a population in a shaded coffee plantation or a diverse homegarden, but a queen emerging from a forest patch might be able to establish a reproductive colony in one of these habitats, at least temporarily, and provide fertile queens that are able to reach another forest habitat patch (Perfecto & Vandermeer 2002). In the Brazilian Atlantic forest, isolated subpopulations of the endangered muriqui monkey, *Brachyteles arachnoids*, are almost certain to experience local extinctions from the relatively small forest patches that house them (Strier 1999). At the regional level, the survival of this endangered species will depend on the ability of the

monkeys to migrate from patch to patch, yet the patches are surrounded by intensive coffee monocultures, treeless degraded pastures, and very extensive monocultural plantations of *Eucalyptus*, none of which is likely to be crossed by migrating muriqui monkeys. A transformation of the agroecological matrix in this region might be our only hope to save the muriqui from having its normal local extinction processes turned into a global extinction of the species. These examples along with many other recent studies (Jonsen *et al.* 2001; Bender & Fahrig 2005; Donald & Evans 2006; Vaughan *et al.* 2007) leave no doubt that the agroecological matrix is of primary importance for the movement of forest species among forest patches.

Agricultural Intensification: Changes in Biodiversity with Management

Approximately 90% of the terrestrial surface of the earth is outside of reserves and is used or managed by human beings in one way or another (Western & Pearl 1990). In the tropics approximately 70% of the land is in pastures, agriculture, or a mixture of managed landscapes (McNeely & Scherr 2003). In the popular and romantic conceptualization of nature as a “Garden of Eden,” many conservationists think of agriculture as the defining feature of biodiversity loss. The world gets divided into those areas untouched or minimally touched by *Homo sapiens* as contrasted to those areas despoiled by human activity (Terborgh 1999).

One of the main observations that caused a reevaluation of this prejudice was the correlation between the decline of populations of songbirds in the Eastern United States and the transformation of the coffee agroecosystem of Central America. The traditional method of coffee production includes a diverse assemblage of shade trees with the coffee bushes growing in the understory (Perfecto *et al.* 1996). These coffee plantations are important winter

habitats for migrant birds from North America (Greenberg *et al.* 1997; Tejeda-Cruz & Sutherland 2004). This key observation has been significant in demonstrating that agricultural ecosystems can be critical repositories of biodiversity, but, even more importantly, that the particular type of agricultural practice was a determinant of the biodiversity it contained (Perfecto *et al.* 1996, 2003; Moguel & Toledo 1999; Perfecto & Armbrrecht 2003; Donald 2004). Not all coffee plantations harbor high levels of biodiversity, and the characterization of what types of agroecosystems generally harbor greater or lesser amounts of biodiversity has only recently emerged as a serious scientific question.

When dealing with managed ecosystems it is first necessary to distinguish between two concepts of biodiversity. First is the collection of plants and animals that the manager has decided are part of the managed system—rice in the paddies of Asia, corn and beans in the traditional fields of Native American Mayans, carp in the fish ponds of China, and so on. This is referred to as the “planned” biodiversity, sometimes called the “agribiodiversity” (Vandermeer *et al.* 2002). Then, there are the organisms that live or spend some time in the managed systems, but are not intentionally included there by the managers—the aquatic insects and frogs in the Asian rice paddies, the birds and insects that eat the Mayan’s corn and beans, the crayfish that burrow their way into the sides of the Chinese fishponds. This is referred to as the “associated” biodiversity (Vandermeer *et al.* 2002). Frequently, the managers themselves are determinedly concerned about the planned biodiversity, especially when dealing below the species level (i.e., genetic varieties of crops). However, it is almost certainly the case that the associated biodiversity is the most abundant component of biodiversity in almost all managed ecosystems, and as such, it has received a great deal of attention in recent years. Furthermore, the associated biodiversity also may have important functions in the

agroecosystem (Giller *et al.* 1997; Vandermeer *et al.* 2002).

The process of intensification of agriculture provides a conceptual framework for analyzing the role of agriculture in the conservation of biodiversity, especially when concerned with associated biodiversity. Although the term “agricultural intensification” has a very specific and complex definition in economic history and anthropology, in the biodiversity literature the term “management intensification” or “agricultural intensification” is taken to be the transition from ecosystems with high planned biodiversity to low planned biodiversity and an increase in the use of agrochemicals and machinery (Perfecto *et al.* 1996; Giller *et al.* 1997; Donald *et al.* 2001; Vandermeer *et al.* 2002; Perfecto *et al.* 2003; Wickaramasinghe *et al.* 2004; Tscharnkte *et al.* 2005; Philpott *et al.* 2006). In the case of coffee, for example, intensification refers to the reduction or complete elimination of shade trees accompanied by an increase in the application of synthetic fertilizers and pesticides (Perfecto *et al.* 1996). The ecology of the agroecosystems is such that the final stages of intensification usually include the application of agrochemicals to substitute the functions or ecosystem services of some of the biodiversity that is eliminated.

When examining the relationship between agriculture and biodiversity conservation, one of the main questions of concern is what is the pattern of associated biodiversity change as a function of the intensification of agriculture? This question remains largely unanswered for almost all agroecosystems and almost all taxa. From the few studies that have examined this question (Guiller *et al.* 1997; Donald *et al.* 2001; Perfecto *et al.* 2003; Söderström *et al.* 2003; Semwal *et al.* 2004; Wickaramasinghe *et al.* 2004; Tscharnkte *et al.* 2005; Philpott *et al.* 2006), it is possible to make one generalization: there seem to be two basic patterns of associated biodiversity change as a function of intensification (Perfecto *et al.* 2005; Fig. 1). First, associated biodiversity declines by only

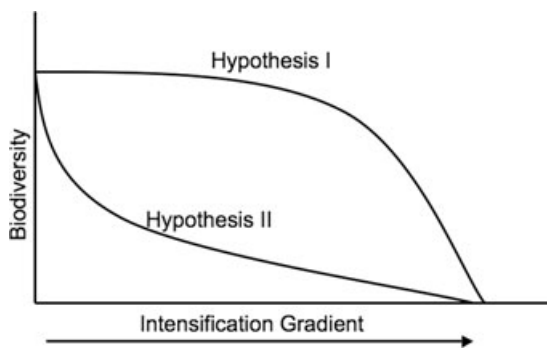


Figure 1. Two hypotheses about the relationship between management intensity and biodiversity.

small amounts with low levels of intensification, and only much higher levels of intensification result in dramatic declines (hypothesis I in Fig. 1). Second, as frequently assumed by many conservationists, associated biodiversity falls dramatically as soon as a natural habitat is disturbed by some agricultural intervention (hypothesis II in Fig. 1). Which of these two patterns (or what combination of the two) exists in particular systems is largely unknown for most taxa.

Conservation biologists often fail to fully acknowledge a component of agricultural intensification that can have devastating consequences for biodiversity—pesticide applications. Extinction of the world's small organisms should cause as much concern as the extinction of charismatic megafauna (Wilson 1987). Insects, mites, nematodes, microbes, and representatives from at least 30 different kingdoms of organisms abound in the soils, leaf litter, and other niches in every environment in the world and are highly susceptible to pesticides (molecular phylogenies indicate that older systems of six or fewer kingdoms are anachronistic, e.g., Lecoindre & Le Guyader 2006). An old cotton field in Nicaragua contains almost no ants, as far as our personal informal faunal surveys could determine (Perfecto, unpublished data). Ants in these fields (and most other insects, except those that have evolved resistance) have gradually disappeared due to the massive spraying of pesticides in a failed 30-year exper-

iment with industrial agriculture that not only did not bring riches to the Nicaraguan people, but also contaminated the land for many years after cotton was abandoned (Metcalf 1980).

Recent studies of amphibians have helped to focus this issue. In a study examining the effect of the herbicide Roundup® on the larvae of three species, Relyea (2005) reported over 90% mortality rates. Similarly, applying this herbicide to adults of the same species, he found close to 70% mortality for one of them, and smaller but significant effects on the others. These results were surprising given that glyphosate, the active ingredient in Roundup®, had been reported to have minimal toxicity on vertebrates (Smith & Oehme 1992). However, the commercial formulation of this herbicide contains a surfactant to ensure that the active ingredient adheres to the leaves of plants, and it appears to be the combination of these ingredients that causes the high mortality of amphibians (Relyea 2005). Regardless of the details about the mortality mechanism, the main conclusion of Relyea's study is clear and robust—one of the world's most extensively used herbicides kills amphibians. Given the dynamic turnover pattern of many species of frogs and salamanders and the fragmented nature of most terrestrial ecosystems, it is essential that they must be able to move through the agricultural landscape to find new ponds (Werner *et al.* 2007). The introduction of Roundup® into the agroecosystem might thus condemn many amphibian species to extinction. Furthermore, the expansion of Roundup®-ready transgenic soybean production in Brazil, Argentina, Paraguay, and Bolivia (Kaimowitz & Smith 2001; Trigo & Cap 2003; Pengue 2005) may have devastating effects on the amphibian diversity of South America.

In addition to the direct mortality effect of Roundup® on amphibians, there is a potential indirect effect of pesticides reducing migration of many organisms through the agricultural landscape, which could easily tip the balance of the basic metapopulation equation toward a global extinction (Hanski 1999).

Intensification, Food Production, and the Conservation of Biodiversity

The increasing demand for food has led some agriculture and development advocates to argue that the best option to meet the challenges of increasing food production and conserving wildlife is to increase yields by intensifying agriculture to spare land for conservation (Borlaug 1987, 1997; Waggoner 1994; Waggoner *et al.* 1996; Cassman 1999; Trewavas 2002). Although this is not a position taken by most ecologists or conservation biologists, it has been supported by some (Robinson 1994; Southgate 1994; Green *et al.* 2005). Donald (2004) argues that for some crops the loss of pristine habitat to low-intensity agricultural systems often has less of an impact on biodiversity than the intensification of these systems. For these crops, such as coffee, cacao, and rice, increasing demand can be met by increasing the area cultivated under low-intensity systems, with little impact on biodiversity (Donald 2004). On the other hand, Donald (2004) also argues that for other crops, no production method gets close to matching natural habitats in terms of biodiversity and therefore meeting future demand without harming biodiversity can be achieved only with intensification. A similar argument is made by Green and colleagues (2005), who assert that most organisms have a density–yield function which would result in hypothesis II in Figure 1, and therefore agricultural intensification combined with land sparing would be the best option for conserving biodiversity and meeting food demands.

These positions are based on two assumptions. First, that agricultural intensification leads to land sparing, and second, that there is a productivity tradeoff, in other words, that the biodiversity value of farmland (including organic and agroecological methods) declines with increasing yield (Balmford *et al.* 2005; Green *et al.* 2005). These two assumptions need to be examined more carefully.

Intensification does not take place in a social/political vacuum. Frequently, regions that experience agricultural intensification also experience increased economic activity, higher demand for products and services, immigration, road construction, and in many cases higher deforestation rates (Wiersum 1986; Barraclough & Ghimire 1995; Foster *et al.* 1999; Angelsen & Kaimowitz 2001b; Lee & Barrett 2001; Morton *et al.* 2006). Furthermore, intensification frequently results in the displacement of small farmers and agricultural workers, who then move into nearby marginal land or the agricultural frontier and cause more deforestation (Kaimowitz & Smith 2001; Wright & Wolford 2003; Schelhas & Sánchez-Azofeifa 2007). For a more detailed discussion of the intensification–land sparing debate, see Box 1.

The second assumption of the intensification–land sparing argument is that there is a productivity–biodiversity tradeoff, in other words, that those agricultural technologies that increase yields decrease biodiversity. The assumption is effectively true in the case of industrial agricultural production systems, especially those following Green Revolution technologies. However, the situation is more complicated when examining other, more complex agricultural systems. For example, reviews comparing organic and conventional agriculture present evidence that, on average, low-input/organic farming has the potential to produce as much as industrial farming, but without the negative environmental impacts (Stanhill 1990; Pretty *et al.* 2003; Halberg *et al.* 2005). Other studies report on specific cases in which organic farming is less productive (e.g., Lockeretz *et al.* 1981; Mäder *et al.* 2002; Trewavas 2004), and polemics can be cited on both sides of the issue. However, most recently Badgley *et al.* (2007) reviewed over 300 studies that compared “organic-like” productive activities with conventional and found that, while individual studies could be cherry picked to support either side of the issue, on average there is no evidence that conventional methods outperform organic ones in terms of productivity. These organic/agroecological

Box 1. Agricultural Intensification and Land Sparing

The assumption that agricultural intensification leads to land sparing is seductive in its simplicity. Given an arbitrary area, we begin by assuming that there is a target, T , for production of some commodity in that area. Then we can easily construct a simple production function that associates the proportion of land in production with total production on that land, in which case we always see an increasing pattern, usually with diminishing returns (see any economics textbook, for example, Simon & Blume 1994). That function will have its value at all points in the domain increased with intensification (by definition), which is to say $f_1(x) < f_2(x)$ where f_2 refers to the production function after intensification. Then $P = f(x)$, where x is the fraction of area in production and P is the total agricultural production. To meet the target production of T , we see that the amount of land necessary to put into agriculture is $f_1^{-1}(T)$ before intensification and $f_2^{-1}(T)$ after intensification, and thus intensification always requires less land. This simple formulation can be embellished with all sorts of other interesting parameters, such as discount rates, land rents, input market uncertainties and many others (see, for example, Green *et al.* 2005). We have added, for example, to this basic idea the value of biodiversity itself (Perfecto *et al.* 2005).

The problem is not with the actual model and certainly not with the more sophisticated elaborations of the basic idea. The problem is with the initial framing of the problem. Rarely is it actually of interest to know what a “target” for production is. Vague notions such as the calorie requirements of the world, have little to do with decisions that are made at the farm or even regional levels. Indeed, in most parts of the world, if there is a “target” it is to maximize return on investment, which is only indirectly related to a production target. Farmers frequently fail to engage in particular practices not because they are less productive, but rather because they require a large cost for labor or capital outlays. In the end, the framing of an area with the duo “land sparing” (or set asides, or preserves, or refuges) and “agriculture with improved technology” is wrong to begin with. Of course working from within that framing it is difficult to avoid the conclusion that if $f_2(x) > f_1(x)$ then $f_2^{-1}(T) < f_1^{-1}(T)$ —less land will be required in agriculture if it is intensified, thus leaving more land for set-aside. But it is sophistry, even if unintended.

Angelsen and Kaimowitz (2001a) take a far more sophisticated approach, noting that there is a fundamental contradiction that is sometimes ignored. First, “the belief that technological progress in agriculture reduces pressure on forests by allowing farmers to produce the same amount of food in a smaller area has become almost an article of faith in development and environmental circles.” Second, “. . . basic economic theory suggests, that technological progress makes agriculture more profitable and gives farmers an incentive to expand production on to additional land.” Angelsen and Kaimowitz (2001a) report on detailed studies that sometimes support one, sometimes the other, point of view. We conclude that the “article of faith” that “progress in agriculture reduces pressure on forests” is not supported by data.

In a more extensive work, Angelsen and Kaimowitz (2001b) edited a series of chapters that include 17 case studies from Latin America, Africa, and Asia. Their conclusions from all these studies is that the issue of intensification of agriculture and its relationship to deforestation is complex and, effectively, that agricultural policy could be modified in such a way as to promote forest-preservative policies rather than policies that, however unintentionally, actually promote more deforestation with “improved” agricultural technologies. We return later, when we speak of grassroots social movements, to the qualitative nature of the sorts of agricultural development models that restrain deforestation.

However, using the case studies presented in Angelsen and Kaimowitz (2001b), it is difficult to avoid the general conclusion that, for the most part, conventional agricultural technological improvement causes more deforestation. Granted the situation is complicated by many factors, and it is certainly sometimes the case that improved agricultural technology has decreased deforestation rates. But examining closely the 17 case studies presented, in 12 of them there was a clear indication that technological change had an effect on deforestation. Of those 12, nine showed increasing deforestation as a result of intensification or new agricultural technology (three of the nine suggested it could go either way, depending on circumstances), and only three suggested a necessary decrease in deforestation with intensification. All cases were treated with the complex analysis they deserve, and in our view, negate the assumption that increases in agricultural technology leads to land sparing. For example, in speaking of the Atlantic Coast of Costa Rica, Roebeling and Ruben (2001) note that increases in productivity of cattle land tended to increase deforestation while increases in productivity of maize production

had the opposite effect. Holden (2001) notes that in Northern Zambia, changes in agricultural technology seem to first have the effect of decreasing deforestation but later, as populations expand either from local population growth or migration, the effect is the reverse. In their summary, Angelsen and Kaimowitz (2001b) observe that agricultural planners and conservationists alike need to take account of the kind of technological advancements proposed, of the nature of the technological improvements envisioned along with the sociopolitical background so as to attempt the so-called “win-win” solution of increasing the well-being of rural people while at the same time decreasing the rate of deforestation. It is never a simple equation of IF $f_2(x) > f_1(x)$ THEN $f_2^{-1}(T) < f_1^{-1}(T)$.

systems (including organic agriculture, natural systems agriculture, permaculture, and many others) have been shown to be generally more biodiversity-friendly than conventional farming systems (for a meta-analysis see Bengtsson *et al.* 2005). Taken in combination, these studies strongly suggest that a biodiversity–productivity tradeoff is not a *sine qua non*. In other words, it is possible for some highly productive farming systems to maintain and promote biodiversity. As we discuss in detail below, it is not only the conversion from a native habitat to agriculture that matters for biodiversity conservation, but also the conversion of agriculture from a biodiversity-friendly type to a biodiversity-unfriendly type that accounts for most biodiversity loss within agricultural landscapes.

Yet, as we argued in a previous section in this paper, there is another important way in which agriculture and biodiversity are related, one that belies the simple formula of the intensification–land sparing dichotomy. Most biodiversity should not be thought of as “point source,” or, as ecologists refer to it, as *alpha* (local) diversity. Rather, the collection of those points, the general landscape, or, as ecologists refer to it, the *beta* biodiversity, must be taken into account. As we have already argued, the evidence regarding local extinctions even within large fragments of natural habitats and the importance of the agricultural matrix in facilitating or preventing inter-patch migrations suggest that agricultural landscapes dominated by diverse, organic (and in most cases agroforested) systems is

frequently our best bet for biodiversity conservation. These farming systems provide a high-quality matrix through which migrations may occur, thus counteracting the extinction rates of populations that invariably exist in a metapopulational context (Jonsen *et al.* 2001; White *et al.* 2002; Bender & Fahrig 2005; Donald & Evans 2006; Vaughan *et al.* 2007). This suggests that a research/development priority should be to develop high-productivity agroecological systems, in other words, the intensification of organic and diversity-friendly agricultural systems (Balmford *et al.* 2005; Matson & Vitousek 2006; Badgley *et al.* 2007). We agree with Pichon *et al.*, (2001) that “. . . rather than introducing or developing new technologies or techniques aimed at increasing productivity to reduce forest clearing, agricultural researchers should concentrate more on improving the endogenous systems that settlers already use to obtain steady and stable returns.”

Biodiversity and Tropical Agriculture—What the Data Say

Although the role of agriculture in the conservation of biodiversity was largely ignored by earlier conservation biologists, recent years have seen increased attention to managed systems. Here we review the role of agroecosystems as habitat for biodiversity as well as a matrix that can facilitate migration between patches of forests or other natural habitats. We divide the review into two main categories: 1) planned biodiversity (or what is frequently

called agrobiodiversity) and 2) associated biodiversity.

Planned biodiversity: Here we only briefly summarize a tremendous literature in three standard categories—homegardens, annual systems, and perennial systems (agroforestry systems, including treecrops with shade trees and silvopastoral systems).

Homegardens are land-use systems involving multipurpose trees and shrubs in association with annual and perennial agricultural crops as well as livestock (usually small animals) that are intensively managed by family labor within the compound of individual houses. Frequently, and especially in the humid tropics, these systems are very diverse, have multiple canopy strata and multiple functions (Fernandes & Nair 1986; Coomes & Ban 2004; Kehlenbeck & Maass 2004; Major *et al.* 2005; Montagnini 2006; Peyre *et al.* 2006; Pandey *et al.* 2007). Due to the diversity in extent, plan, and operation (Watson & Eyzaguirre 2001; Quat 1995; Wickramasinghe 1995; Ceccolini 2002), qualitative and experimental research in agroforestry has been limited. Although most of the research in homegardens is qualitative and descriptive, more recent research using cluster and other multivariate quantitative analyses (e.g. Blanckaert *et al.* 2004; Albuquerque *et al.* 2005; Kehlenbeck & Maass 2004; Peyre *et al.* 2006) complements earlier descriptive work and provides a more comprehensive picture of the role of homegardens in the conservation of biodiversity.

Most studies of homegardens, whether descriptive or quantitative and experimental, demonstrate that these agroforestry systems have a high planned biodiversity (Kumar & Nair 2006). Analyzing 10 selected homegardens from different ecological and geographic regions, Fernandes and Nair (1986) showed that the average size of homegardens is less than half a hectare, yet they contain a high planned biodiversity composed of a large number of woody and herbaceous species structured to form two to five vertical canopy strata, with each component having a specific place

and function; they reported a range from 191 plant species (152 woody species and 39 herbaceous species) in a Javanese *Pakarangan* system, to 14 species (7 woody species and 7 herbaceous species), in a Ka/Fuyo garden of the semi-arid region of Burkina Faso. Montagnini (2006) gives several examples from studies of plant diversity in homegardens in Mesoamerica, reporting between 334 and 80 species contained therein. Smith (1996) notes that in the Brazilian Amazon, traditional homegardens contain a remarkable diversity of plants, estimating over 70 perennial species in cultivation and new ones continually being adopted from the natural forest. Other studies of Amazonian homegardens also report a high diversity of plants, both wild and domesticated species (Coomes & Ban 2004; Major *et al.* 2005). Even in some semi-arid regions, homegardens have been reported to have high planned species diversity. For example, in a study of 31 homegardens in northeastern Brazil, almost 400 plant species across all gardens were reported (Albuquerque *et al.* 2005). Homegardens have also been noted to be close mimics of the surrounding forests with their multistrata vertical canopy layers (Blanckaert *et al.* 2004; Das & Das 2005; Hemp 2005). A few studies have examined beta diversity and have reported variable levels of similarity depending on the regions compared. For example, Pandey and colleagues (2007) reported between 82% and 93% similarity in plant species between homegardens within the Andaman Islands of India, while the plant species similarity was only 12% to 18% when comparing homegardens in Andaman with those in the Nicobar Islands. Kehlenbeck & Maass (2004) report a different spectrum of species cultivated in homegardens among three villages in Sulawesi, with Sørensen coefficients ranging from 61% to 74%.

Although not specifically focused on agrobiodiversity, Salafsky (1994) provides a useful distinction between homegardens, which in and of themselves can be extremely diverse in both operation and biodiversity, and forest gardens (*sensus* Padoch 1992). Forest gardens occupy

a position more or less intermediate between homegardens and secondary forest, seemingly partly a product of abandoned homegardens and partly of incursions into natural forests. They will clearly contain a significant amount of biodiversity, although as noted by Salafsky (1994), their diversity tends to be restricted since productive activities tend to be concentrated on a limited number of productive tree species (e.g., durian, sugar palm).

Eyzaguirre and Watson (2001) emphasize the utility of homegardens as repositories of genetic agrobiodiversity, noting the socioeconomic and cultural drivers involved in their maintenance. Through years and generations, farmers select and cultivate the useful plants, effectively doing *in situ* conservation of genetic and species diversity and turning their homegardens into reservoirs of current and potential resources and gene pools for the eroding indigenous species (Blanckaert *et al.* 2004; Das & Das 2005; Pandey *et al.* 2007). Through these means, homegardens preserve not only biodiversity but also cultural diversity and local cultural histories and become sites for domestication and preservation of useful species (Toledo *et al.* 1995; House & Ochoa 1998; Blanckaert *et al.* 2004; González-Soberanis & Casas 2004; Das & Das 2005; Peyre *et al.* 2006; Pandey *et al.* 2007).

A variety of studies have documented the loss of planned biodiversity with the intensification and higher levels of commercialization within homegardens (Soemarwoto 1987; Fey 1988; Gillespie *et al.* 1993; Peyre *et al.* 2006). Examining this process in homegardens in the state of Kerala in India, Peyre and colleagues (2006) reported that, while 50% of the studied gardens still displayed traditional features, 33% had incorporated modern practices, which include a decrease in the tree/shrub diversity and a gradual concentration on a limited number of cash-crop species. Intensification usually involves the homogenization of garden structure and increased use of external inputs, including pesticides, which invariably have a negative effect on biodiversity (Kumar & Nair 2004). On the

other hand, a study of homegardens in the *terra preta* (Amazonian Dark Earth) soils found that while commercialized homegardens increased dominance of highly marketable species, they were nevertheless able to maintain high species diversity (Major *et al.* 2005).

Thrupp (2000) and Montagnini (2006) tie the agrobiodiversity of homegardens to a more general strategy of food security. All homegardens produce at least some of the food that is consumed by the family, and many produce cash crops, medicinal plants, firewood, timber, or livestock fodder (Fernandes *et al.* 1985; Fernandes & Nair 1986; De Clerk & Negreros-Castillo 2000; Wezel & Bender 2003; Hemp 2004; Kehlenbeck & Maass 2004; Kumar & Nair 2004; Major *et al.* 2005; Peyre *et al.* 2006). In Nicaragua, Méndez and colleagues (2001) found that families obtain more than 40 different plant products from homegardens.

Homegardens are not static but have evolved over centuries in response to socioeconomic dynamics (Michon & Mary 1994; Coomes & Ban 2004; Kumar & Nair 2004; Peyre *et al.* 2006). These agroforestry systems have been producing sustained yields for centuries in a resource-efficient way and are considered economically efficient, ecologically sound, and biologically sustainable (Fernandes & Nair 1986; Kumar & Nair 2006). Additionally, homegardens tend to produce multiple products, including firewood and wood for construction, lessening the pressure on nearby forests (Das & Das 2005). Finally, homegardens can also be refuges of wild biodiversity. For example, Griffith (2000) reported that during the 1998 El Niño-associated fires in the Petén region in Guatemala, homegardens and other agroforestry systems may have provided critical refuges for wildlife. Because of their importance for the livelihood of many families in rural areas of the tropics, especially the humid tropics where the majority of the hotspots of biodiversity are located, homegardens should be considered an important component of integrated landscape conservation strategies.

Annual systems are usually thought of as either monocultures or polycultures, the former constituting the classical grain-production systems of the world, as well as many modern technified systems. Wheat, rice, and maize, in modern agriculture, are typically grown as monocultures and thus the agrobiodiversity is minimal. On the other hand, many crops, including basic grains, are frequently grown in diversified polycultural or intercropping systems, especially in the tropics (e.g., Willey 1979; Vandermeer 1989; Gurr *et al.* 2003; Altieri & Nicholls 2004). In China more than 28 million hectares are annually sown in intercropping systems (Liu 1994). Vandermeer (1989) lists a minimum of 55 distinct combinations of annual crops that are commonly found grown together in the tropics. Nevertheless, these annual intercropping systems usually contain only two or three crops in association with one another, relegating the idea of planned diversity to a trivial status. Consequently, the question of planned biodiversity in annual systems has largely focused on the issue of functionality, only indirectly related to the conservation of biodiversity.

Earlier literature made it clear that increased production (also called “overyielding”) was common but not ubiquitous in intercropping systems (Vandermeer 1989). The mechanisms for overyielding have been debated but are pretty obvious from basic ecological theory. Two crops that completely share an ecological niche are not expected to combine in such a way as to increase productivity, but if they somehow exploit different niches, overall use of the available environment would be more efficient. Because of the close association of this idea with Gause’s principle that no two species can occupy the same niche, this idea has been referred to as the “competitive production principle” (the parallel principle in ecology is the competitive exclusion principle) (Vandermeer 1989). For example, on nitrogen-deficient soils the combination of grasses and legumes is known to overyield because of legume nitrogen fixation (Stern 1993; Knudsen *et al.* 2004) and the con-

sequent ability of the legume to take advantage of nitrogen stores (atmospheric) not available to the grass. Subsequently, the issue reemerged as a debate in the nonagricultural ecological literature (e.g., Tilman & Downing 1994; Naeem *et al.* 1996; Tilman 1996; Huston 1997; Tilman *et al.* 2001b; Loreau *et al.* 2002). What seems to be clear is that legumes and grasses together do, in fact, increase productivity, most likely because each species samples a slightly different pool of nitrogen, so the system as a whole samples a larger resource base than either alone (Snaydon & Harris 1979). However, there is little evidence that annuals, or short-lived perennials offer any production advantage stemming from resource usage when grown in combination, beyond the legume/grass association (Trenbath 1999; Huston *et al.* 2000; Wardle & Grime 2003), even though the debate remains active (e.g., Hooper *et al.* 2005). On the other hand, a novel yield-enhancing mechanism of intercropping, not considered in the biodiversity and ecosystem functioning debate, has recently emerged. Li and colleagues (2007) demonstrated maize–faba bean overyielding in phosphorous-deficient soils due to the uptake of phosphorous mobilized by the acidification of the rhizosphere via faba bean root release of organic acids and protons.

Furthermore, it is also clear that other aspects of annual intercropping, beyond the simple joint utilization of resources, come into play. Protection from pests and diseases is high on the list of reported functions of intercropping (Risch 1980; Abate *et al.* 2000; Landis *et al.* 2000; Schroth *et al.* 2000; Finckh & Karpenstein-Machan 2002; Rämert *et al.* 2002; Altieri & Nichols 2004). It is generally thought that one of two mechanisms operates to generate this function (Root 1973): 1) the combination of crops acts to disrupt the ability of the pest to find its host, or 2) the combination of crops encourages natural enemies into the system. It is also the case that both of these mechanisms could be occurring at the same time and act to obscure one another (Vandermeer 1989).

Both intercrop overyielding and the crop protection effect of diverse cropping systems contribute indirectly to biodiversity conservation. By increasing yields, intercropping systems can contribute to the livelihood of farmers and release pressure to convert forest into agriculture. Also, by reducing pest damage, intercropping can reduce the use of toxic chemicals that harm biodiversity (Giller *et al.* 1997; Krebs *et al.* 1999; Johnsen *et al.* 2001; Benton *et al.* 2003; Relyea 2005). Finally, the diversification of these annual cropping systems, even if it is an intercrop of two or three crop species instead of one, can increase certain taxa of associated biodiversity, such as ants, wasps, and spiders (Provencher & Vickery 1988; Perfecto & Sediles 1992; Nampala *et al.* 1999).

Perennial systems, the majority of which are agroforestry systems, are in and of themselves very diverse in tropical regions. Indeed, an entire scientific journal is devoted to the analysis of agroforestry (*Agroforestry Systems*) and many books have been written about it (e.g., Nair 1985, 1993; Young 1989; Current *et al.* 1995; Nair & Latt 1998; Buck *et al.* 1999; Schroth & da Fonseca 2004; Batish *et al.* 2007), most of which include some discussion of the planned biodiversity of agroforestry. Most of these volumes treat agroforestry systems as general ecological systems in which trees and crops interact with one another, not specifically from the point of view of agrobiodiversity, but all appreciate the diversity of agroforestry types, which brings up the issue of classification (Nair 1985; Gordon *et al.* 1997; Leakey 1996; Sinclair 1999). Casting classification systems based on either ecological or economic function is ultimately useful for general purposes, to be sure (Sinclair 1999). However, for purposes of biodiversity evaluation we use a modified system that seems useful explicitly for biodiversity analysis. Thus we consider three categories 1) silvopastoral systems, 2) tree crops with shade, and 3) trees above annual crops.

Silvopastoral systems, the combination of pastures and trees, have been common in the

tropics, although systematic summaries of their functioning are normally contained within reviews of agroforestry more generally (but see Murqueitio *et al.* 2004). Surveys from all tropical areas indicate that silvopastoral systems are common and offer great potential ecological services if managed properly (Dagan & Nair 2003). From the point of view of biodiversity per se, it is most convenient to view silvopastoral systems on a double gradient, density and diversity of overstory trees. For example, on a single farm in Nicaragua, one can wander through the farm, all of which is available and utilized by cattle, and find areas that are relatively devoid of trees, areas that have a high density and diversity of overstory trees (composed of both remnants from the original forest and volunteers that emerged and were maintained by the farmer), and areas that have a high density and low diversity (mainly areas with a relatively high density of a particular species such as citrus trees) (Perfecto I., personal observations). This simple observation suggests the dual classification of tree density and tree diversity (Leakey 1996), and largely begs the question, what is the role of silvopastoral systems in biodiversity conservation? They are, for the most part, diverse in the sense of trees and grasses, and the planned biodiversity questions are largely confined to questions of interaction between trees and pasture, with ecosystem service potentials having more to do with nutrient cycling, carbon sequestration, and biomass production, but not closely related to biodiversity per se (Fisher *et al.* 1994; Pagiola *et al.* 2004). On the other hand, a broader landscape-level approach to biodiversity conservation in recent years has highlighted the role of silvopastoral systems as a matrix that can maintain biodiversity and facilitate the movement of organisms between patches on natural habitat (Saunders & Hobbs 1991; Harvey & Haber 1999; Dagan & Nair 2003; Pagiola *et al.* 2004; Harvey *et al.* 2006).

Since pastures are one of the main managed ecosystems in the tropics (McNeely & Scherr 2003), it is important to manage these

systems in a way that will promote biodiversity. There is no doubt that the combination of trees and pastures is better for biodiversity than intensive or highly overgrazed pasture monocultures, especially if the trees in the system are native. In their study in Costa Rica, Harvey and Haber (1999) documented 5583 trees, belonging to 190 species, in 237 hectares of pastures. In this study primary forest tree species accounted for 57% of all the species and 33% of all the individuals encountered. Silvopastoral systems also favor associated biodiversity (Harvey *et al.* 2004, 2006), which will be discussed below.

The combination of tree crops with shade trees has become a most common way of thinking of biodiversity and agroecosystems, perhaps because of its almost canonical representation of natural systems agriculture (Beer 1987; Jackson 2002; Perfecto & Vandermeer 2008). Of the many combinations probably the most commonly cited are coffee, cacao, and rubber, which, in all three cases include a frequently diverse assemblage of trees, chosen by the farmer (or sometimes left from the original forest), for a variety of productive or ecosystem services purposes (Rice & Greenberg 2000; López-Gómez *et al.* 2007; Méndez *et al.* 2007; Philpott *et al.* 2008). While it is generally assumed that the systems involving shade trees along with tree crops are ecologically benign or even helpful in the conservation of biodiversity, some authors have emphasized potential negative effects under certain circumstances. While it is clear that agroforests generally provide a refuge for biodiversity (Perfecto *et al.* 1996), it is also occasionally the case that agroforests represent a stage in the process of further deforestation (Mary & Michon 1987). For example, Lawrence's (1996) analysis of rubber gardens in West Kalimantan, Indonesia is significant in its attempt to analyze not only the tree-species diversity protected in this agroforestry system, but also the general tendency for biodiversity loss on a regional scale as local farmers make particular decisions about favoring rubber trees as their economic base.

A variety of systems in which trees are planted in conjunction with crops have been extensively analyzed (Kang 1993, 1997; Salazar *et al.* 1993), not necessarily from the point of view of biodiversity, but rather from a functional point of view—what is the advantage of growing trees with crops. A particularly influential idea (Cannell *et al.* 1996), formulated as “the central agroforestry hypothesis,” held that for agroforestry to present an advantage over monocultural production, it was necessary that the trees must acquire resources that the crop would not otherwise acquire. The particular system of alley cropping (trees grown in one or several rows and crops planted between the row clusters of trees) has been extensively studied at research stations around the world. Sánchez (1995) provided a critical review of those studies, suggesting that their worth was not empirically justifiable, a point of view that was not completely accepted by all workers (e.g., Vandermeer 1998).

Associated biodiversity: As we noted previously the intensification of agriculture has come to be a conceptual base for examining the role of agriculture in biodiversity studies, with the central hypotheses revolving around the question, what is the pattern or patterns of biodiversity loss (or gain) along the intensification gradient (see Fig. 1)? There are now a large number of studies, especially in the coffee agroforestry system, demonstrating that the loss of biodiversity with the intensification of agriculture is variable depending on the taxa examined, but usually not the extreme form originally proposed by preservation-minded conservationists (Perfecto *et al.* 2003; Schulze *et al.* 2004; Schroth & Harvey 2007). Our study of ants along the coffee-intensification gradient in Costa Rica and Mexico (Vandermeer & Perfecto 2000), is typical, the results of which are reproduced in Figure 2.

Several review articles have already summarized the results of dozens of biodiversity studies in the coffee agroecosystems (Perfecto *et al.* 1996; Moguel & Toledo 1999; Perfecto & Armbrrecht 2003; Perfecto *et al.* 2007; Philpott

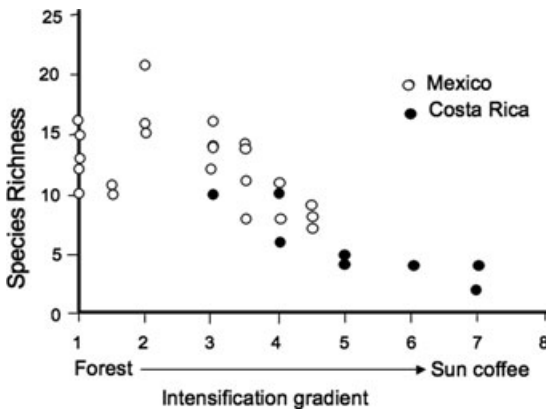


Figure 2. Ant species diversity as a function of the intensification gradient in coffee plantations in Costa Rica and Mexico (from Vandermeer & Perfecto 2000).

et al. 2008). In general, these reviews provide solid evidence that associated biodiversity (soil microorganisms, epiphytes, ants, butterflies, beetles, spiders, birds, bats, rodents, amphibian, and reptiles) decreases with a decrease in the density and diversity of shade trees, although the pattern of species loss varies depending on the taxonomic group investigated. A recent meta-analysis using data for ants, birds, and trees supports these results and provides more rigorous evidence for both the biodiversity conservation potential of the shaded coffee agroforests and the loss of diversity with coffee intensification (Philpott *et al.* 2008). Although biodiversity research in the cocoa shaded system is not as well developed as that in coffee, a number of studies have been published in the last few years. A recent special feature of the journal *Biodiversity and Conservation* (volume 16, number 8) focused on the biodiversity conservation potential of shaded cocoa systems from a broad geographic range in the tropics. These studies show results similar to those for coffee: shaded cocoa systems harbor higher diversity than other agricultural land use systems but lower diversity than primary forests; tree diversity (i.e., the planned biodiversity) varies with the type of management, location, socio-economic, cultural, and other factors (Schroth and Harvey 2007); and

associated biodiversity (mostly animal diversity) is usually correlated with tree diversity and shade cover (Bos *et al.* 2007; Delabie *et al.* 2007; Harvey & González Villalobo 2007; Van Bael *et al.* 2007). As in coffee, some taxa show similar levels of diversity between shaded cocoa and adjacent forests (Perfecto & Vandermeer 2002; Bos *et al.* 2007; Delabie *et al.* 2007), and in some cases the diversity is similar but the species composition is different, highlighting the importance of maintaining a mosaic of land-use systems, including forests, for the conservation of the highest levels of biodiversity (Bos *et al.* 2007).

Both coffee and cacao agroforests, especially the most diverse systems, have been demonstrated to be high-quality matrices (i.e., a land-use system that facilitates the migration of organisms from habitat patches) (Perfecto & Vandermeer 2002; Vaughan *et al.* 2007). For example, in Costa Rica, two species of sloth frequently use shaded cacao plantations to move among forest fragments as well as a source of food and resting sites (Vaughan *et al.* 2007).

Studies on associated biodiversity in silvopastoral systems also demonstrate the importance of scattered trees and live fences for the movement of organisms within the agricultural landscape and between forest fragments (Estrada & Coates-Estrada 2001; Stoner 2001; Harvey *et al.* 2006). Other studies demonstrate, in general, the importance of tree cover in pasture for biodiversity conservation. In the pasture-dominated landscapes of Rivas, Nicaragua, Harvey and colleagues (2006) reported that due to their tree cover and remnant riparian forests and secondary forests, this agricultural landscape contained more than 50% of the bat, dung beetle, and butterfly fauna, and 40% of the bird fauna found in the nearest reserve. Other studies have demonstrated the biodiversity benefits of live fences, isolated trees, and windbreaks in pasture-dominated areas (Guevaras *et al.* 1994; Hinsley & Bellamy 2000; Barrance *et al.* 2003; Harvey *et al.* 2004, 2005).

Few studies have examined associated biodiversity in homegardens, but those that have

report high levels usually associated with planned plant diversity and structural complexity (Fang *et al.* 1999; Blanckaert *et al.* 2004; Hemp 2004; Albuquerque *et al.* 2005). For example, the multistrata Chagga homegardens on Mount Kilimanjaro harbor more than 70% of all Saltatoria (Insecta: Orthoptera) forest species and more than 50% of endemic species (Hemp 2004). However, a few species were found only in remnants of submontane forests, suggesting that these species are highly affected by habitat loss and homegardens alone cannot be presumed to maintain species diversity for all Saltatoria (Hemp 2004). In an intensively farmed rural landscape in Hubei Province in subtropical China, homegardens were found to harbor among the highest density and diversity of earthworms of any of the other systems examined (Fang *et al.* 1999). A study of homegardens in Mexico demonstrates the interactions between homegardens and the surrounding vegetation. A variety of wild species invade the gardens and are not removed if they are considered useful (Blanckaert *et al.* 2004), and sometimes the farmer begins protecting or even cultivating them. The gardens of San Rafael Coxcatlán-Mexico showed a remarkable number of wild medicinal plants growing spontaneously in the gardens (Blanckaert *et al.* 2004).

Social Movements and the Conservation of Biodiversity

Much as traditional agriculturalists have given tremendous insights to the development of agroecological principles, there has been a recent, if underreported, surge of interest on the part of small farmers in the tropics in biodiversity conservation (Pretty & Smith 2004; Bacon *et al.* 2005; Cullen *et al.* 2005; Campos & Nepstad 2006; Bawa *et al.* 2007). Indeed, our experience is that small farmers in the tropics are frequently surprised to hear that some conservationists regard them as the enemies of conservation and the main cause of tropical defor-

estation. Although there is no doubt that landless peasants are partially responsible for the expansion of the agricultural frontier in areas like the Amazon (Fernside 1993) and the tropical rain forests of Central America (Kaimowitz 1996), blaming them for tropical deforestation is an oversimplification that ignores the political economy of agricultural development in tropical countries (Vandermeer & Perfecto 1998). Decades of environmentally destructive megaprojects, such as the colonization of the Amazon in Brazil, transmigration projects in Indonesia, and the establishment and expansion of banana plantations in Costa Rica and Ecuador, along with an uneven distribution of land, have been the principal cause of tropical deforestation (Hecht & Cockburn 1989; Ozorio de Almeida 1992; Sponsel *et al.* 1996; Vandermeer & Perfecto 2005). Government policies that benefited a landed minority, owners of large rural estates, and in many cases foreign corporations, displaced small farmers from the best agricultural lands, effectively giving them two options: to move to the cities, or to migrate to the agricultural frontier (Moran 1996; Stonish & DeWalt 1996; Wright & Wolford 2003). However, in many developing countries the small farmers and the landless are getting organized and demanding access to land and their right to a decent livelihood. These farmers' organizations, increasingly organized under the banner of food sovereignty, sustainable agriculture, and conservation of biodiversity, are an integral component of the discourse. Organized groups such as *Via Campesina*, a coalition of over 100 small farmer and peasant organizations from around the world, are now taking an active role in planning conservation activities and developing alternative agriculture (Desmarais 2007). Brazil's Landless Rural Workers' Movement (MST), the largest rural social movement in the world, actively encourages and teaches agroecology (Wright & Wolford 2003), which includes protection of biodiversity and the development of sustainable agricultural principles. At the 2003

meeting of the Mesoamerican Society for Biology and Conservation, Wilson Campos, a leader of *Via Campesina* in Costa Rica spoke of the acknowledged responsibility of small farmers to conserve the environment and, specifically, biodiversity for future generations.

Realizing the need to work hand in hand with the small farmers who manage the agricultural landscapes in the tropics, some environmental NGOs are beginning to pioneer conservation programs in collaboration with these progressive social movements. An excellent example of the kind of work that incorporates social justice and conservation in a highly fragmented tropical landscape is the work that the Institute of Ecological Research (IPE) is doing in the region of the Atlantic forest in Brazil (Cullen *et al.* 2005). In the Pontal de Paranapanema, a large fragment and several smaller fragments of Atlantic forest form the Morro del Diablo reserve, surrounded by large cattle pastures and settlements established long ago by landless people and currently highly productive. More recently yet further unproductive cattle pastures have seen land takeovers by landless people, some organized by the MST (Cullen *et al.* 2005). Rather than seeing the MST as their enemy, IPE began collaborating with the MST to diversify and increase the forest cover on the farms in the settlements, as well as to improve the livelihoods of the families involved. Initiatives like this will, in our view, contribute to the creation of an agricultural matrix that is socially just and politically stable and that will conserve biodiversity at the landscape level and in the long run.

It is important to note that what we are proposing here is qualitatively different from the integrated conservation and development programs (ICDP) that attracted so much investment by bilateral development agencies and the Global Environmental Facility (GEF) during the 1990s, and which generated debate in the development conservation literature (Oates 1999; Rabinowitz 1999; Terborgh 1999; Wilshusen *et al.* 2000; Brechin *et al.* 2002;

McShane & Wells 2004). Although these programs began by addressing the need to look beyond reserve boundaries and to pay attention to the welfare of the local communities, they retained institutional, top-down approaches and stopped short of recognizing the pivotal role of rural social movements as protagonists the new conservation. But more importantly for our argument, the ecological processes involving extinction and migration were not fully appreciated. It does not matter how ineffective the ICDP programs were if the underlying ecology demands a landscape approach, which we argue that it does.

Conclusion: Agroecology, Social Justice, and a New Conservation Paradigm

As agriculture becomes a dominant feature in tropical regions, the effective conservation of biodiversity will depend, not only on protected areas, but also on the agricultural matrix and in particular on how the systems within it are managed. Many studies now offer evidence that diverse agricultural systems can harbor high biodiversity, including a large proportion of forest species. Furthermore, the quality of the agricultural matrix is emerging as an important component of the new conservation paradigm, given that most of the habitats in the tropics are fragmented (Gascon *et al.* 2000), and many populations are likely to have a metapopulation structure. In particular, many of the studies reviewed above point to the importance of planned biodiversity and especially tree cover within agricultural landscapes in the tropics. This conclusion is supported by other studies in the humid tropics (Daily *et al.* 2001, 2003; Estrada & Coates-Estrada 2001, 2002; Petit & Petit 2003; Harvey *et al.* 2006; Schroth & Harvey 2007; Vandermeer & Perfecto 2007). A stronger emphasis on the agricultural matrix leads inevitably to the role of farmers in the conservation of biodiversity and the realization that rural social movements are at the vanguard

of this new conservation paradigm (Desmarais 2007).

Conservationists in the past have focused on the purchase and protection of large tracts of land to be set aside as nature preserves with surrounding areas acting as buffers. From what we now know about how biodiversity is structured ecologically, this is a doomed strategy if pursued in isolation. While there is no rational need to convert any more forests to agriculture, they are in fact being converted and the future almost certainly will present us with mainly fragmented landscapes. It is in those fragmented landscapes that the world's biodiversity will be located. A long-term plan for biodiversity conservation needs to acknowledge that fact and work at the landscape level to not only focus on preservation of the patches of native vegetation that remain, but to construct a landscape that is "migration friendly." That landscape is most likely to emerge from the application of agroecological principles. Those principles are most likely to be enacted by small farmers with land titles. Small farmers with land titles are a consequence of grassroots social movements (Rosset 2006). Metaphorically, we see a dichotomy of visions, with one side purchasing land in pristine areas to be protected by armed guards and the other side marching with the poor in their struggle for revolutionary change. Naturally this is something of a caricature, but does capture the two poles of thought that we encounter when we read and talk with people concerned with biodiversity conservation in the tropics. And it is clear, we hope, which side we are on. Indeed, we suggest that these new rural social movements in fact hold the key to real biodiversity conservation. Joining the struggle of the millions of small farmers all over the world is more likely to yield biodiversity benefits than buying some patch of so-called pristine forest.

Conflicts of Interest

The authors declare no conflicts of interest.

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