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**The Role of Forest Biodiversity
in the Sustainable Use of
Ecosystem Goods and Services
in Agro-Forestry, Fisheries, and Forestry**

Proceedings of International Symposium
for the Convention on Biological Diversity

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Forestry and Forest Products Research Institute

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Ensuring food production: native biodiversity provides pollination and biological control services

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Abstract

Land use intensification drives extinctions of species and alters the ways in which they interact with one another. This loss of biodiversity may result in reduced rates of ecosystem services such as pollination and biological control, with loss of functional group and response diversity having the greatest effects on function. Biodiversity also acts as insurance in changing conditions, so in addition to reduced mean rates of ecosystem services, stability of these services may also decline. Similarly, alterations to the dynamic structure of networks of interactions among species may affect their resilience to other environmental changes. Conservation of natural forests, as well as ‘softer’ agricultural/silvicultural systems can help to conserve regional biodiversity, which can enhance ecosystem functioning in adjacent managed habitats. Conservation of heterogeneous landscapes, including natural forests, will be necessary to maintain ecosystem services in the face of a suite of interacting global environmental changes.

Keywords: Global environmental change; ecosystem service; insect; land use change; food web.

Introduction: land use change and biodiversity loss

Sixteen years after the Convention of Biological Diversity first came into force, forests and their associated biodiversity continue to decline. Almost 6 million hectares of forest are destroyed each year in the humid tropics alone (Achard et al. 2002). One of the strongest predictors of forest loss is human population density (Wright and Muller-Landau 2006), which continues to grow in most regions, particularly those with high biodiversity (Cincotta et al. 2000).

The primary driver of forest loss is clearance for agricultural land use, with humans now appropriating more than a third of total terrestrial net primary production (Foley et al. 2005, Foley et al. 2007, Haberl et al. 2007). These land use changes take place at multiple scales, with an increasing proportion of available land being sequestered for agriculture, and a concomitant increase in the management intensity of agricultural land (Tscharntke et al. 2006). This produces not only a loss in total forest cover, but also a loss of landscape- and habitat-scale heterogeneity in vegetation structure.

These changes in land use are the greatest driver of biodiversity loss globally (Sala et al. 2000), and it is estimated that current extinctions are occurring at between 100 and 1000 times pre-human rates (Pimm et al. 1995). In addition to the obvious moral tragedy of these losses, elevated extinction rates have engendered concern about the effects of species losses on the functioning of ecosystems and the consequences for human wellbeing (Lawton 1994, Chapin et al. 2000). Clearly the loss of certain species such as crops or medicines (i.e. material goods) could be devastating, and the variety of ecosystem services (Myers 1996, Daily et al. 2000) that natural ecosystems provide to humans are estimated to be worth almost twice the global GNP (Costanza et al. 1997). However, what has been less clear is whether the loss of biodiversity per se is important for maintaining ecosystem services, or whether we should be more concerned about the loss of certain economically or functionally important species.

Here I will summarise the impacts on ecosystem services of lost biodiversity through continued deforestation. Specifically, I will focus on the effects of biodiversity loss on pollination and biological control of pests, two ecosystem services involved in food production (Fig. 1). These services are not trivial, as 76% of our food crops (35% of food volume) depend on animal pollination (Klein et al. 2007), and natural enemies provide an estimated \$4.5 billion worth of pest/disease control each year in the US alone (Losey and Vaughan 2006). In addition to changes in these ecosystem services, I will examine evidence that biodiversity may promote resilience in services under changing environmental conditions. Finally, I will discuss strategies for conserving functional diversity in order to maximise the provision of ecosystem services.

Biodiversity and ecosystem services

The last decade and a half has seen an exponential increase in the number of studies examining the effects of biodiversity on rates of ecosystem functions or processes (Fig. 2). Many of the early studies were conducted in experimental grassland plots, and generally found a positive effect of species diversity on plant productivity (Hooper et al. 2005). These effects can sometimes be due to the fact that more diverse assemblages are more likely to contain, by

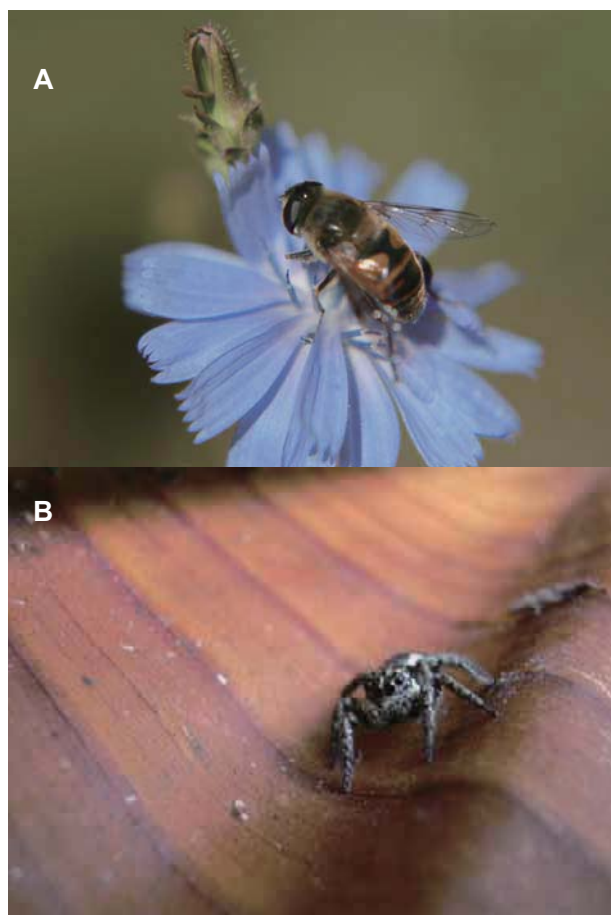


Fig. 1 Ecosystem service providers. A) Pollinators such as this hoverfly (in an apple orchard, Region del Maule, Chile) can be critical for the reproduction of both crop and wild plants. B) Predators such as spiders (here in a coffee plantation, Manabi, Ecuador) can be important regulators of insect pest populations.

chance alone, a particularly productive species (Huston 1997, Cardinale et al. 2006). This lottery or 'selection' effect would suggest that, provided we know which species are important, the loss of other species would have little impact on ecosystem functioning. However, not only would this assumption ignore the likelihood that species can become more or less important at different times or under different conditions (see 'Biodiversity as insurance in fluctuating environments' section below), but there is also evidence that species diversity per se can affect primary productivity through niche complementarity (Hooper et al. 2005, Cardinale et al. 2007). Under this mechanism, different species utilise slightly different resources, or obtain them in slightly different ways. This reduces competition within species, allows fuller exploitation of the available resources/niches, and maximises rates of an ecosystem process (Hooper et al. 2005, Cardinale et al. 2007).

In addition to this work on plant biomass production, recent evidence suggests that high diversity of animals that provide ecosystem services, such as biological control and pollination, can

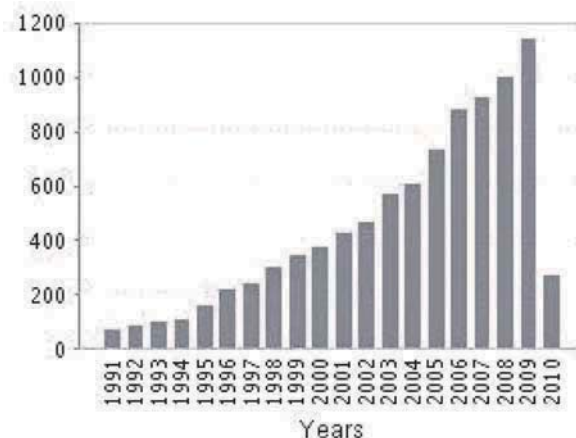


Fig. 2 Increasing number of studies testing effects of biodiversity on ecosystem functioning per year. Data compiled from Web of Science database on 14 April 2010 using search terms (biodiversity or "species richness" or "species diversity") and ("ecosystem function*" or "ecosystem service" or "ecosystem process" or "productivity" or "primary production" or biomass or "parasitism rate" or "predation rate" or pollination).

enhance food production. For example, Cardinale et al. (2003) showed that diverse insect predator communities were twice as effective as single species at reducing populations of aphids on alfalfa, and this improvement in biological control even doubled alfalfa yield. Similarly, Snyder et al. (2006) found that diverse control agents were more effective at controlling two species of aphids on collards, and that reduced aphid densities resulted in increased plant growth. Diversity of animal pollinators can also improve fruit set and crop yields. For example, high diversity of pollinators has been shown to increase pollination success and yield of a variety of food crops, including coffee (Klein et al. 2003), tomato (Greenleaf and Kremen 2006), and watermelon (Kremen et al. 2002).

The benefits of biodiversity are greatest when species differ in their functional characteristics, thereby providing diversity of functional groups as well as species (Elmqvist et al. 2003, Luck et al. 2003). For example, pollinator assemblages where several species differ significantly in their morphology and/or pollinating behaviour can be most effective at pollinating crops, particularly when the flowers are variable in their location or time of opening (Hoehn et al. 2008). A recent study of pumpkin grown in Indonesian homegardens found that pollinator species differed in their functional traits, such as preferred pollinating height, time of day at which they were most active, body size, and the way in which they carry pollen. Therefore, diverse pollinator assemblages contained a greater diversity of these traits, and were consequently able to pollinate all the pumpkin flowers more successfully than assemblages with fewer species (Hoehn et al. 2008). In fact, when

Hoehn et al. (2008) used multivariate methods to group pollinator species into functional groups based on their physical and behavioural differences, the diversity of functional groups was a stronger predictor of pollination success (the number of seeds per pumpkin) and yield (the size of the fruit), than was pollinator species diversity.

Such examples provide evidence that biodiversity loss can have important consequences for real-world food production. However, for niche complementarity to occur, there must be a variety of niches available to be partitioned among functional groups (e.g., the different height and timing of flowers in the study of Hoehn et al. 2008). Therefore, we may hypothesise that the effects of biodiversity on ecosystem process rates will be greatest when habitats or resources are heterogeneous, i.e. when there are a variety of different resource niches available. This hypothesis was tested recently for three different ecosystem processes in three different systems: biomass production in German grassland communities, parasitism rates by wasps in a range of habitats in Ecuador, and coffee pollination in Sulawesi, Indonesia (Tylianakis et al. 2008b). The authors found that, in all three cases, the positive effect of biodiversity (of grasses, parasitoids, and pollinators) on process rates (biomass production, parasitism, and pollination respectively) increased with increasing heterogeneity of the limiting resource (soil nutrients, host larvae, and coffee flowers; Tylianakis et al. 2008b). This suggests that the benefit of biodiversity for ecosystem services such as pollination and biological control will be greatest in heterogeneous natural and seminatural ecosystems, such as those found in agroforests and forests.

In addition to the direct benefits of animal (pollinator and natural enemy) diversity for pollination and biological control, plant biodiversity within or adjacent to production systems can provide benefits for food production. First, diverse plants provide a variety of floral resources to sustain diverse pollinator communities, and an array of herbivorous insects to provide prey for natural enemies. Thus, it is not surprising that diversity of herbaceous plants has been shown to correlate positively with diversity of bees and wasps (Tylianakis et al. 2006a), or that pollinator diversity can help to maintain diverse plant communities (Fontaine et al. 2006). These insect species can be abundant in forests, but also move out into adjacent crops, providing high rates of pollination (Ricketts et al. 2004, Blanche and Cunningham 2006, Blanche et al. 2006; but see Chacoff et al. 2008) and biological control (Landis et al. 2000) close to forest habitats. In addition to the benefits of plant diversity for maintaining abundant animal service providers, plants may also increase the per-capita efficacy of these animals. For example, many parasitoids of pest insects feed on the pest during their larval stage, but require floral nectar during their adult phase. Providing non-crop floral resources adjacent to crops

can enhance the longevity and fecundity of parasitoids, thereby enhancing biological control (Tylianakis et al. 2004). This phenomenon is well-studied in arable crops, though its potential for the enhancement of biological control in forests and agroforests has received less attention.

Biodiversity as insurance in fluctuating environments

The above examples highlight the importance of biodiversity for maintaining high (average) rates of functions/services such as biological control or pollination. However, as important as having high rates of food production, is the necessity of stability of food resources, both through time and in the face of environmental changes. The effects of biodiversity on stability have received considerable research attention (May 1973, McNaughton 1978, Givnish 1994, Hanski 1997, McGrady-Steed et al. 1997, Hughes and Roughgarden 2000, Worm and Duffy 2003, Hooper et al. 2005, Ives and Carpenter 2007), with measures/definitions of stability varying widely across studies (Pimm 1984, Grimm and Wissel 1997). In terms of pollination and biological control services, greatest attention has been paid to reducing temporal variability. By occupying distinct temporal niches, pollinator or natural enemy species can cause, through statistical averaging, a reduction in temporal variance of pollination or pest control (Yachi and Loreau 1999). For example, Kremen et al. (2002) found that the importance of different wild pollinator species changed from year to year, meaning that sites with higher pollinator diversity experienced sustained pollination through time. Similar effects have been shown for attack rates by insect parasitoids, where temporal variability is reduced by parasitoid diversity (Tylianakis et al. 2006b). Biodiversity can also theoretically increase the resilience of ecosystem services (Petersen et al. 1998, Elmqvist et al. 2003) by buffering against environmental change (McNaughton 1978). The strength of this buffering or 'insurance' effect depends on the degree of asynchronicity in the responses of individual species to environmental fluctuation, and on the specific nature of their responses (i.e. response diversity; Yachi and Loreau 1999, Elmqvist et al. 2003).

It is also important to recognise that the world is experiencing a suite of environmental changes simultaneously (Sala et al. 2000), and that the effects of these changes on ecosystems may not be independent of one another (Folke et al. 2004, Tylianakis et al. 2008a). For example, land use intensification may allow generalist invasive species to become dominant and further affect native biodiversity (Didham et al. 2007). Ultimately, any strategies for conserving biodiversity will need to consider the interrelated nature of the drivers of species loss (Folke et al. 2004), and recognise that mitigation of the effects of one driver may require

actions to reduce another (Didham et al. 2007).

Analogous to these temporal insurance effects is the spatial insurance effect of biodiversity in patchy environments (Loreau et al. 2003). In mosaic landscapes, different species occupy different habitat types. This turnover of species among habitats is called beta diversity, and can contribute significantly to the overall (gamma) diversity of a region (Tylianakis et al. 2005). In addition to providing high overall diversity, beta diversity may be important for maintaining spatial insurance in pollination or biological control (Loreau et al. 2003). Similarly, even when a given species occupies multiple habitats, it can move between patches, becoming an important service provider in some patches or at certain times (e.g., promoting recovery following disturbance; Lundberg and Moberg 2003), even though it may be less abundant or important in others (Srivastava and Vellend 2005). Thus, spatial and temporal occurrence and turnover in biodiversity can provide resilience in ecosystem services (Bengtsson et al. 2003, Tscharrntke et al. 2007), but species turnover in time and space may be reduced by land use intensification at the landscape scale (Tylianakis et al. 2005).

Interactions between species

Many ecosystem services (including pollination and biological control) involve interactions among two or more species. Interactions between species are determined by the relative abundance of different participant species, their behaviour, phenology, etc, and this vulnerability may mean that we observe changes in species interactions before the species involved actually go extinct (Janzen 1974, Tylianakis et al. 2008a). A recent review of almost 700 studies measuring responses of over 1000 pairwise species interactions to different drivers of global environmental change found that pollination interactions tend to decline in strength or frequency with land use change, particularly habitat fragmentation (Tylianakis et al. 2008a). In contrast, effects on insect predator-prey and parasitoid-host interactions were much more variable, making future changes in the success of biological control difficult to predict. Even more variable was the change in interactions with different drivers of environmental change. Pollination tended to be negatively affected by all drivers tested, but responses of insect natural enemy interactions varied considerably across drivers (Tylianakis et al. 2008a). As mentioned above, the effects of these drivers are not independent, and the modification of habitats can alter interactions between invasive species and their native competitors, further facilitating invasion (Didham et al. 2007). For example, intensification of cacao agroforests can promote invasion by exotic ants, which then reduce the diversity of native forest ants disproportionately compared with their effects on habitat generalist species (Bos et al. 2008). Although this study did not

test functional effects of ant invasions, loss of forest ant biodiversity could potentially result in a decline in the functions/services they provide.

Despite the importance of changes to biodiversity or mutualistic and antagonistic interactions, pairwise interactions between species do not occur in isolation. Rather, they are components of a larger network of feeding and/or mutualistic interactions, whose structure can be critical for ecosystem stability (May 1973, Paine 1988, Dunne et al. 2002, Kondoh 2003, de Ruiter et al. 2005, Bascompte et al. 2006, McCann 2007), for example, by determining the effects of species extinctions on community-wide pollination success (Bascompte et al. 2003). Various attributes of the structure of these networks can therefore have important implications for conservation (Tylianakis et al. 2010) but the impacts of this structure on stability cannot be predicted from the pairwise interactions alone.

Thus, in addition to local or global extinctions of species, there may be less obvious, insidious effects of agricultural change on the interaction structure of ecosystems. Although methods for quantifying these interaction networks have been around for more than a decade, it was unclear until recently what effect, if any, land use changes have on food web structure. A study of 48 quantitative networks of feeding interactions ('food webs') involving bees, wasps and their natural enemies in Ecuador, showed for the first time that the species interactions comprising the "web of life" are sensitive to changes in land use (Tylianakis et al. 2007). Conversion of forests to intensive agriculture led to a sizeable shift in food web structure, and subsequent dominance of the webs by one or two interactions resulted in bees and wasps suffering heavy attack rates from their natural enemies (particularly an introduced parasitic wasp). This increase in parasitism of pollinators and insect predators could have significant effects on the ecosystem services that these species provide.

A number of subsequent studies have examined the responses of networks of parasitoid-host or pollinator-plant interactions to land use change and habitat fragmentation (Albrecht et al. 2007), species invasions (Lopezaraiza-Mikel et al. 2007, Aizen et al. 2008), and climate change (Memmott et al. 2007). Unfortunately, pollinator-plant networks are usually examined independently from parasitoid-host networks (but see Henson et al. 2009 for an impressive exception), when the interplay between these two functions may in fact determine crop productivity. Moreover, in addition to altering the overall structure of the network, anthropogenic disturbances such as land use changes may homogenize the dynamic structure (i.e. spatial and temporal variability) of networks at the regional scale (Laliberté and Tylianakis 2010). By splitting the 48 parasitoid-host food webs of Tylianakis et al. (2007, see above) into monthly time steps, Laliberté & Tylianakis (2010) found that the structure of

interactions within the webs was more similar across sites and through time in the (most intensive) rice and pasture habitats. Conversely, forested sites (including managed and abandoned coffee agroforests) had network structures that were highly variable through time and space. This reduction in spatial and temporal interaction turnover with land use intensification is analogous to the reduction of species turnover (beta diversity, see above), and could reduce the insurance value (and resilience) of networks in heterogeneous landscapes or under changing conditions.

Strategies for conserving functional biodiversity

The above sections have provided evidence for the widespread loss of biodiversity, ecosystem services, and change in interaction structure of communities following deforestation and land use intensification. The simplest strategy for stemming this tide of extinctions and loss of ecosystem services would be widespread reforestation and reduction in the extent and intensity of agricultural management. Obviously, the pressures of a growing human population will prevent this from occurring everywhere, so we must be pragmatic in our conservation approaches. Usually only regions with high per capita GDP can afford restoration programmes, producing a strong correlation between a nation's wealth and whether its annual net change in forest cover is positive or negative (Ewers 2006). Therefore, developing countries could be less likely to receive any of the ecosystem service benefits (discussed above) that forest preservation may bring, even though they may be more dependent on these services due to the costs of attempting to replace them with pesticides or machinery.

The first priority must obviously be maintenance of as much of the remaining natural forest cover as possible. In addition to the conservation of protected 'set-aside' areas (which cannot be substituted), softer agricultural or silvicultural practices can provide significant benefits for biodiversity and the ecosystem services associated with food production. For example, appropriately managed organic agriculture can sustain higher diversity than conventional systems for a variety of taxa (Bengtsson et al. 2005). It is often thought that this comes at a cost of reduced yields, but Badgley et al. (2007) compared yields of organic vs. conventional systems in different food categories for 293 datasets. For most categories, the ratio was slightly < 1 for developed countries and > 1 for developing countries (Badgley et al. 2007), indicating that organic crops may even deliver higher yields, in addition to higher per unit revenue. Moreover, certain agricultural systems may be inherently better reservoirs for biodiversity. For example, agroforests (Fig. 3) are often characterised by high species diversity (Perfecto et al. 1996, Moguel and Toledo 1999), including large numbers of specialist species



Fig. 3 Agroforest systems. A) Traditional shade-grown coffee (Manabi, Ecuador) can be a valuable refuge for biodiversity, but B) intensification by removal of shade trees (Boquete, Panama) may reduce these benefits.

(Tylianakis et al. 2005), and food web structures that do not differ significantly from those of natural forests (Tylianakis et al. 2007, Laliberté and Tylianakis 2010). In fact, coffee agroforests have even been found on occasion to contain higher species diversity than native forest (Teodoro et al. submitted). However, the benefits of systems such as agroforestry for biodiversity will depend on the way in which they are managed. Clearing of flowering herbs from the ground of coffee agroforests could reduce bee and wasp diversity (Tylianakis et al. 2006a), and reducing the diversity and density of shade tree species in cacao agroforests can cause a reduction in bee diversity (Tschardt et al. 2008) and increase the spread of, and harm caused by, invasive species (Bos et al. 2008). Thus, even systems that are inherently 'biodiversity friendly' may cease to generate benefits when managed intensively (such as during the transition from shade- to sun-grown coffee, Fig. 3).

Clearly, not all agricultural systems can harbour high levels of functional biodiversity. Yet, appropriately managed agricultural landscapes can still benefit ecosystem services (Tschardt et al.

2005), and landscape diversity effects may even overwhelm local (farm) scale management (Schmidt et al. 2005). For example, the species associated with natural forests or even non-intensive agroforests can move into adjacent more intensive systems, providing ecosystem services (Landis et al. 2000, Ricketts et al. 2004). Therefore, the maintenance of these habitats within a mosaic landscape may provide benefits beyond the area that they require. However, it is worth noting that the conservation value of these systems (particularly native forests) may suffer through time as pest, weed or predator species that are abundant within the crop spill over into more natural systems (Rand et al. 2006). Finally, even landscapes that do not contain natural habitats can still be managed to maximise biodiversity and resilience. By maintaining a variety of crops, and hence a heterogeneous mosaic landscape, beta diversity among crop patches may contribute to high regional diversity of beneficial species (Tylianakis et al. 2005, Tylianakis et al. 2006a, Tschamntke et al. 2007), and provide a ready source of ecosystem service providers to recolonise after disturbance (Lundberg and Moberg 2003), thereby promoting resilience. In fact, conservation programmes such as the European 'agri-environment' schemes may even be most effective in partially modified landscapes (Tschamntke et al. 2005).

Conclusions

The societal and economic impacts of biodiversity loss (Costanza et al. 1997, Chapin et al. 2000, Daily et al. 2000) are only just beginning to be felt. Here I have focused on two ecosystem services (pollination and biological pest control) that are critical for food production, yet there are many more services that will be affected (Myers 1996, Daily et al. 2000). Not only are the average levels of ecosystem services affected by biodiversity loss, but also their stability through time and in response to environmental changes are likely to suffer (e.g., Elmqvist et al. 2003). Land use intensification is one of several drivers of global environmental change, the effects of which are likely to be interactive in many cases, potentially causing self-reinforcing feedbacks between biodiversity loss and one or more other drivers (Chapin et al. 2000, Didham et al. 2007). Conservation of remaining natural forest habitats will be necessary for slowing the global loss of biodiversity. In addition, softer, 'wildlife-friendly' (Green et al. 2005) forms of agriculture, including agroforestry, can be used as an additional refuge for biodiversity, provided that they are managed appropriately. Finally, entire landscapes must be managed as heterogeneous mosaics to maximise spatial and temporal insurance in ecosystem services (Loreau et al. 2003, Lundberg and Moberg 2003, Tschamntke et al. 2005).

Invariably, expansive monocultures that create a homogeneous environment at the farm and landscape scale will be inimical to the maintenance of ecosystem

services and their stability in the face of foreseeable changes to global environmental conditions.

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