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Iterative increase of economic tree species in managed swidden-fallows of the Amazon

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Abstract. Fallow utilization schemes are becoming increasingly popular in agroforestry designs. However little attention has been given to the fate of valuable fallow plants after the end of the initial fallow cycle, and over successive fallow cycles on a regional or inter-fallow level. Evidence is presented here for the spontaneous long-term community enrichment of an area with valuable plants in a cyclic or iterative fashion, in the context of an existing fallow utilization scheme in the Amazon. Review of the ecological processes which operate at microsite, field and community levels indicate that:

a. Due to valuable plants left uncut in the swidden, seeds from valuable species are better able to survive the burn, and may experience a favored germination and establishment because of reduced competition, enhanced fertility of the young swidden, nutrient input from litterfall, and reduced soil temperatures and soil moisture evaporation.
b. The much greater frequency of suitable germination and establishment sites in and around canopy gaps created by management practices during the fallow cycle interacts with a spatial and temporal distribution of fruit trees which may encourage a specific optimal foraging strategy among large numbers of frugivores. The net effect of this interaction would be to decrease competition for, and increase efficiency of, seed dispersal into the large number of available establishment sites.
c. A greater opportunity for frugivore generated seed shadows exist in managed fallows due to the larger number of trails in and around these sites, which are used as flyways.
d. A presence of the more efficient 'specialist' fruit tree seed dispersal strategy in managed fallows – as opposed to the 'opportunist' strategy – which produces patterns of seed dispersal more beneficial to the plant, and may have a longer more evenly spread fruiting season; which, along with relatively large numbers of trees would encourage frugivores to 'camp out' on the resource, depositing seeds nearby.
e. The existence of 'relict' plant species that reflect pre-historic forest management which has led to long term and persistent effects on forest tree species composition.

Introduction

Presently much attention is being placed on investigation and improvement of traditional subsistence farming systems which are able to provide sustained yields in tropical countries [Horowitz 1986; Rambok 1980]. This interest has arisen in the face of alternative (imported) systems failing to provide permanently greater agricultural production. One such improvement with significant agronomic potential is the utilization of the fallow cycle of swidden (slash and burn) agriculture [Denevan and Padoch 1987; Hart 1980; Harris 1971; Barrera et al. 1977; Eden 1980; Basso 1973; Raintree and Warner 1986; Manner 1981; Hiraoka 1985; Gliessman 1981; Weaver 1979; Posey 1985; Janzen 1973]. The general thrust of the majority of this work has been to describe and/or experiment with assemblages of plants which are inserted into appropriate stages of fallow succession. However little attention has been given to the fate of valuable fallow plants after the end of the initial fallow cycle, and over successive fallow cycles on a regional or inter-fallow level. Obviously the difficulty of such a study lies in the great deal of time which would be required to monitor a typical single long-fallow cycle in the humid tropics (20–30 years). Nevertheless, review of the ecological processes which operate at microsite, field and community levels in the context of fallow cycle utilization, can provide insight into the long-term potential productivity of proposed fallow agroforestry schemes.

This paper discusses the potential lasting effects of an existing fallow management design in the Peruvian Amazon, in the context of local ecological processes which promote an increasing abundance of spontaneously occurring, economically valuable plants in a cyclic or iterative (swidden-fallow-swidden-fallow etc.) fashion. Evidence is presented which suggests that this particular arrangement results in long-term community enrichment of an area with economic plants of importance.

Following a brief description of the fallow management scheme, and managed fallow ecology, information is drawn from the ecological literature and the author's observations to describe how fallow management practices interact with specific aspects of the local ecology to enrich the fallow with a variety of valuable plants over successive fallow cycles. The evidence presented falls into three broad categories: 1) floristic ecology, 2) the influence of frugivores, and 3) prehistoric evidence and present day examples. For a detailed description of swidden-fallow management the reader is referred to Denevan and Padoch [1987]. The present discussion focuses on the potential long-term spontaneous increase in abundance of valuable plants as a result of this design, and includes suggestions and guidelines for future research.

Swidden-fallow management

The practice of managing a fallow in the Peruvian Amazon begins at the time the forest is cleared for cultivation, when valuable species such as fruit and palm trees, and those used later for timber, are spared during cutting. Then as the swidden undergoes cultivation, perennial species such as pineapple (*Ananas comosus*), banana (*Musa* spp.), and guineo (*Musa* spp.), and larger trees such as umari (*Poraqueiba sericea*), uvilla (*Pourouma cecropiaefolia*), and pijuayo (*Guilielma gasipaes*) among others (see Table 1 for a more complete list) are planted, interspersed among annual cultivars such as manioc (*Manihot esculenta*) or maize (*Zea mays*). These perennials mature more slowly than annual crops, and many will not be ready to harvest until the swidden is older and fading into fallow, or later in the fallow cycle. Such an approach allows for a phased harvest of different crops. Under fallow management, new swiddens are dominated by annual and fast maturing crops, while older swiddens have a greater abundance of slower maturing perennnials and semi-perennials [Denevan and Padoch 1987] which may be better adapted to conditions of declining soil fertility and increased weediness [Manner 1981]. The fallow species (fruit and palm trees) will be ready for harvesting during the fallow cycle. Those trees left uncut during forest clearing will continue to produce during both swidden and fallow cycles. While competition between the swidden and valuable fallow plants at the beginning of the swidden phase would appear to advantage the uncut trees over the annuals, and the annuals over the emerging fallow perennials, it is unknown what the intensity of competition is or what the reduction in crop productivity is due to this competition. Most likely it would depend upon the total number of uncut trees in the swidden. As the swidden cycle proceeds and the annuals are harvested, the competition between the planted fallow perennials and the swidden plants would be reduced to essentially nothing. Planting fallow species at the same time as the annual cultivars are planted allows them to take advantage of the more fertile soil present at the beginning of the cropping cycle when they are young, and ensures that they will be of an adequate size when the cropping cycle is over and weed communities are invading [Denevan and Padoch 1987]. In contrast to traditional swidden abandonment, abandonment in the context of fallow management constitutes a non-distinct transition from swidden to fallow, resulting in a sequence from a cultivated field, to a managed fallow combining economic plants and natural forest regrowth, to a 'forest fallow' in which valuable plants are still greater in number than in the original forest [Denevan and Padoch 1987].

Later in the fallow cycle, management involves protection (cutting away or 'slashing' the surrounding competing regrowth) of useful plants, both planted and spontaneously occurring. The result is a fallow with a combination of perennial herbaceous and tree crops together with natural forest regrowth, which change in composition and proportion at various stages of

Table 1. Useful species for managed fallows

Scientific name	Common name	Use[1]	Source[2]
Allagoptera cf. pseudocalyx	piaçaba	F	1
Alibertia edulis	marmelada (lisa)	F	1
Alibertia sp.	marmeleda do campo	F	1
Anacardium occidentale	cashu	F	2
Ananas comosus	pineapple	F	2
Annona cherimola	annona	F	2
Annona crassiflora	araticum	F	1
Arachis hypogaea	peanut	F	2
Artocarpus incisa	panidilla	F	2
Atrocarpus integrifolia	jacá	F	1
Astrocaryum chambira	chambira	C, H	2
Astrocaryum huicungo	huicungo	C	2
Astrocaryum tucuma	tucum	F	1
Astrocaryum vulgare	tucuma	F	1
Bertholletia excelsa	castanha do Pará	F	1
Bixa orellana	annatto	H	2
Byrsonima crassifolia	muruci	F	1
Calocarpum mammosum	mamey zapote	F	3
Carica papaya	papaya	F	2
Caryocar villosum	piqui	F	1
Cedrela odorata	cedar (tropical)	C	2
Celtis sp.	hackberry	F	3
Citrus aurantifolia	lima	F	1
Citrus aurantium	laranja	F	1
Citrus limon citratus	lemon	F	2
Citrus sinensis	orange	F	2
Cocos nucifera	coconut	F	2
Coffea arabica	Café	F	1
Cordia sp.	cereja Kayapó	F	1
Crescentia sp.	calabash	F	3
Endopleura uchi	uxi	F	1
Erythroxlon coca	coca	M	2
Eugenia jambos L.	jambo	F	1
Euterpe sp.	assai	F, C	2
Genipa americana	genipapo (two varieties)	F	1
Guilielma gasipaes	pijuayo	F, U	2
Hancornia speciosa	mangaba	F	1
Hymenaea courbaril	copal	F	2
Inga sp.	guava	F	2
Inga sp.	Shimbillo	F	2
Iriartea sp.	cashapona	C	2
Iriartea sp.	cumala	C	2
Iriartea sp.	huacra pona	C	2
Jacaranda sp.	huamansamana	C	2
Jessenia bataua	ungurahui	F	2
Lecythis usitata	sapucaia	F	1
Lonchocarpus sp.	barbasco	U	2

Table 1 (continued).

Scientific name	Common name	Use[1]	Source[2]
Mangifera indica	manga	F	1
Manilkara huberi	massaranduba	G	1
Manilkara zapota	sapodilla	F	3
Mauritia flexuosa	aguaje	F, U	2
Mauritia martiana	buritirana	F	1
Mauritia vinifera	buruti	F	1
Maximiliana maripa	inaja	F	1
Musa sp.	banana	F, U	2
Musa sp.	platano	F	2
Ochroma sp.	balsa	U	2
Oenocarpus bacaba	bacaba	F	1
Olmedia sp.	llanchama	H	2
Orgygnia martiana	babassu	F	1
Parinari montana	pariri	F	1
Persea americana	avocado	F	2
Pimenta dioica	allspice	F	3
Phytelephas	yarina	C	2
Platonia insignis	bacuri	F	1
Pouraqueiba sericea	umari	F	2
Pourouma cecropiaefolia	uvilla	F	2
Pouteria caimito	caimito	F	2
Pouteria macrophylla	tuturuba	F	1
Psidium sp.	guayaba	F	2
Ravenata guyanensis	banana brava	F	1
Rollinia mucosa	biribá	F	1
Solanum sp.	cocona	F	2
Spondias lutea L.	cajá	F	1
Theobroma cacao L.	cacau	F	1
Theobroma grandiflorum	capaçú	F	1
Theobroma bicolor	macambo	F, U	2

1. Use Code
   F: Food and Beverage
   C: Construction or Thatching
   H: Handicraft and Dyes
   U: Utilitarian
   M: Medicinal
   G: Attract game

2. Source
   1. Posey, 1985 (Amazon)
   2. Denevan and Padoch, 1987 (Amazon)
   3. Turner and Miksicek, 1984 (lowland Yucatan)

succession [Denevan and Padoch 1987]. Thus instead of a dense secondary forest with a relatively tight canopy, and a predominantly single, distinct life form, like that which occurs in natural rainforest successions [Richards 1964; Kellman 1969] there is a much more patchy stand of fruit trees and other valuable plants, interspersed with a subcanopy of woody shrubs, open areas, and natural forest regrowth [Unruh, unpublished manuscript]. In older managed fallows, clearings or gaps of variable sizes may be cut as valuable timber species – spared when cutting the forest – are removed, or when old fruit trees are cut to make charcoal [Padoch et al. 1985].

Managed fallow ecology

While fallow management activities are directed toward the production of forest crops in the immediate fallow cycle, it is the interplay between management and fallow succession which sets the stage for the cyclic increase in economic species to occur at the community level. Managed fallow ecology is given a more complete treatment in Unruh [1988] but is briefly discussed here in order to describe how fallow management practices result in the right conditions for the cyclic increase in the abundance of valuable plants.

The establishment of woody plants in old swiddens is strongly influenced by microhabitats. Uhl et al [1981; and Uhl 1983; Uhl et al. in press] working in the Rio Negro region of the Venezuelan Amazon, found that after only one year, areas in the shade of fruit trees and fallen logs produced significantly more woody plants than did areas of bare soil. Such a difference appears to be due to seed dispersal by birds and bats, which are attracted to these microhabitats and then excrete seeds there; where environmental conditions for germination and survival are favorable. Live trees, and dead leaves and branches which fall from these trees and other late swidden plants provide nutrients, and reduce evaporation from the soil and lower soil temperatures [Uhl et al. 1981; Uhl 1983; Uhl et al. in press] as would decomposing slash resulting from fallow management later in the fallow cycle. Such localized patches of structure and nutrients are the first sites of establishment for woody species in an abandoned swidden [Uhl et al. in press; Uhl 1987] and these islands of woody vegetation expand until the patches connect with each other and with the regeneration from the surrounding forest [Uhl 1983; Uhl et al. 1981; Richards 1964]. One of the more valuable ecological attributes of swidden-fallow management as an agroforestry system, is the much greater frequency of these microhabitats in old managed swiddens due to trees left uncut while clearing the forest, and the emerging valuable perennials planted early in the cultivation cycle. The presence of these 'nutrient patches' in an aging swidden provide more sites for the early establishment of woody species, conceivably speeding up initial forest regeneration after crop abandonment. In addition, early successional species are often 'large-gap' adapted [Denslow, 1980], and breaking up the gap size, or open area of the old swidden with a large number of such 'islands' might select for the establishment of later successional species more quickly.

Such in-field heterogeneity has an additional advantage. The root-mat – essential to nutrient cycling and in reducing soil nutrient leaching especially in nutrient poor soils – may not be degraded as completely after cultivation in managed swiddens, and may reform much more quickly in young managed fallows. In contrast to the traditionally abandoned swidden with its depleted root-mat [Scott 1978; Uhl et al. 1981] the managed swidden-fallow at the end of the cultivation cycle would have many areas of intact root systems due to the presence of spared valuable trees and emerging late swidden perennials and woody plants.

While swidden-fallow management during the cultivation cycle results in in-field heterogeneity at the end of the cropping period, which may speed initial site recovery, the single most important ecological impact of management in the fallow cycle is the alteration of the spatial location of foliage within the stand (Unruh, unpublished manuscript). Due to selective cutting (or slashing) of vegetation from early in the fallow cycle in order to protect valuable plants, maturing fallows generally have a reduced, more open upper canopy than unmanaged fallows. As a result, more light reaches the forest floor, allowing the germination and growth of understory plants which would have remained as dormant seeds under a fully developed upper canopy. Thus the net effect of management on canopy structure is two-fold: a patchy, open upper canopy, and a much more pronounced understory. The spatial arrangement of foliage in managed fallows changes both stand nutrient cycling and plant succession for the remainder of the life of the fallow. The evidence presented below suggests that these changes encourage a quicker, more prounced soil nutrient recovery.

The nutrient content of slashed vegetation in managed fallows is significantly different from that of leaf litter which is naturally abscised. This is because during leaf senescence, retranslocation of nutrients especially N and P in the tropics, occurs from the leaf to the woody tissue, resulting in lower nutrient concentrations in senesced leaves than in green leaves still attached to the tree [Herrera et al. 1978; Stark 1971; Chapin and Kedrowski 1983]. Slashing secondary regrowth in the management of fallows however prevents this mechanism of conservation of nutrients within the plant, resulting in slashed vegetation having greater concentrations of limiting nutrients than naturally abscised litterfall. This could be a particularly valuable nutrient input to the soil since such cutting takes place in the proximity of useful fallow plants. Such a concentration of recently cut leaves may actually serve to increase local forest productivity much in the same way that the leaf cutter ant (*atta colombica*) does by harvesting and bringing fresh cut leaves to a central point – effectively concentrating P [Lugo et al. 1973; Haines, 1975].

Additional vegetation-soil-nutrient processes that take place in managed fallows include: 1) the participation of a greater quantity of understory vegetation in stand nutrient cycling, vegetation which recent research (in the temperate zone) suggests may have a higher leaf nutrient content than leaves of overstory trees [Yarie, 1980; Chapin and Kedrowski 1983]; 2) a more continuous input of young leaf material – higher in N and P fractions than older leaves [Stark 1971; Chapin and Kedrowski 1983] – into the soil in the proximity of valuable plants, due to the practice of slashing regrowth vegetation at three to four month intervals in the course of management; and 3) a staggered maturation time of quick growing softwood trees (such as *Cecropia* spp. and *Vismia* spp.) which cycle large amounts of nutrients and enrich the soil more rapidly than under later successional stands [Kellman, 1969; Ewel 1971; Bartholomew et al. 1953; Harcomb 1980].

As succession proceeds, micro-site heterogeneity brought about by management practices, continues to play an important role in the ecological functioning of managed fallows. A managed fallow provides, through its patchy nature, an association of successional states which over time constitute a temporally and spatially changing mosaic of micro-habitats. Such a mosaic would be suitable, at any given time, for occupation by a variety of valuable (as well as non-valuable) plants from distinct successional states – both planted and spontaneously occurring – to exist in managed fallows. However this also may result in the persistence of deleterious weedy species as well, which would also be slashed away as they begin to threaten the valuable plants. Patches – open, closed and intermediate – are sites for micro-environmental variations in such parameters as: light, soil moisture, fertility, temperature [Posey 1985], humidity [Denslow 1980], and pH [Scott 1978]. The effects of such variation on germination, seedling establishment, plant growth and succession is well documented [Brokaw 1980; Lebron 1979, 1980; Garwood 1982; Augspurger 1983, 1984; Vazquez-Yanes and Smith 1982; Cheke et al. 1979; Guevera and Gomez-Pompa 1972; Bell 1970; Richards 1952; Poore 1968; Whitmore 1975, 1978; Hartshorn 1978; Bazzaz and Pickett 1980; Kerr and Posey 1984]. It is such heterogeneity which allows for the occurrence of the low shrub-like pineapple plant in close association with large umari and pijuayo trees in managed fallows as late as 30 years after the swidden cycle [Unruh, pers. obvs].

Variations in micro-environment within the managed fallow continue as valuable plants are maintained by slashing away the surrounding vegetation for as long as the plant produces a useful item. Many valuable species are planted together in the swidden stage, and this can result in whole zones of useful plants within the fallow, i.e., fruit and palm tree zones, and patches of peanut, pineapple and coca [Denevan and Padoch 1987]. The length of time that such a zone continues to produce can determine the length of time that the regrowth is cut back and consequently the successional 'distance' between the managed zone or patch, and the developing secondary vegetation.

In older managed fallows, clearings or gaps of variable size may be created as valuable timber species – spared when cutting the forest – are removed, or when old fruit trees are cut to make charcoal [Padoch et al. 1985; Hiraoka, unpublished manuscript]. Posey [1985] recognizes such micro-climatic variation as the principle mechanism for the economic productivity of forest ecotones created by the Kayapó in the Brazilian Amazon.

The effects of the presence of valuable fallow plants (planted or spontaneously occurring) on the course of natural succession would result from management activities which produce gaps in the forest. This might be similar to Richards' [1964] 'telescoped' secondary succession in 'depleted forest', where selective cutting produces gaps which are temporarily colonized by the fast growing, easily dispersed species which dominate early secondary forest.

As economic species are protected, the growth of these valuable plants is spurred and a greater production realized [Denevan and Padoch 1987; Posey 1985; Johns 1988]. The effect of clearings or gaps and stand thining on micro-environmental variables and enhanced plant growth has been widely reported [Liew and Wong 1973; Nicholson 1965; Whitmore 1974; Schulz 1960; Hartshorn 1978; Denslow 1980 and the references cited therein]. Such manipulation can cause increased reproductive and vegetative activity [Johns 1988], and alter species composition at the community level for whole forests [Posey 1985; Alcorn 1981; Gomez-Pompa 1971; Gomez-Pompa and Vazquez-Yanes 1974] and possibly even the evolution of plant species [Gomez-Pompa 1971]. A reduction in competition for light alone would enhance photosynthesis [Edmisten 1970] and may allow plants to live for longer periods of time [Gomez-Pompa and Vazquez-Yanes 1974].

Fruiting patterns and fruiting seasons are also influenced by local environmental variables [Foster 1982]. Fruit production from protected valuable plants may become enhanced through both greater seasonal fruit production (due to lack of competition) [Johns 1988] and the number of times the protected plant fruits due to its longer life in the managed fallow.

Floristic processes of the cyclic enrichment of swidden-fallows

Effects of burning

Recent studies of swidden ecology have pointed out the reduced role of the seedbank in secondary succession after a burn [Uhl et al. 1981; Uhl et al. in press; Brinkmann and Vieira 1971; Young et al. in press]. In fact forest regeneration from seeds in the soil of slash and burn fields is in most cases, poor [Brinkmann and Vieira 1971; Kellman 1980]. A substantial proportion of the remnant plant component is likewise eliminated [Ewel et al. 1981; Uhl et al. in press]. In swiddens which are to become managed fallows however, the situation may be quite different. The buried viable seed component in swidden-fallows, especially those of valuable plants, would be less affected by burning. The presence of valuable trees purposely not cut while clearing the field creates a heterogenous soil micro-climate with respect to soil moisture and fertility. Standing trees in an otherwise bare field would allow patches of moist soil to exist under the shade. Local soil moisture acts as a buffer against heat exchange; the greater the moisture the more heat is required to raise soil temperature to the level required to kill seeds in the soil [Brinkmann and Vieira 1971]. In addition, developed, intact root systems of these trees would not act as a source of subsurface heat transport during and after the burn, as dead root systems in completely cleared fields do [Brinkmann and Vieira 1971]. This allows seeds near valuable trees a greater chance of surviving the burn than seeds elsewhere in the swidden. And it is worthwhile to note that a large number of seeds under these trees would be seeds from the valuable species themselves. These seeds would then be able to take advantage of the reduced competition and enhanced soil fertility of the new swidden, thus gaining a headstart over invading forest regrowth when the field is abandoned.

As the swidden ages, litterfall from the standing plants would add to the nutrient content of the soils beneath these trees, and would protect seedlings from direct heating, and lower the soil surface temperature and soil evaporation. This could conceivably favor the germination and establishment of valuable seeds over seeds of regrowth plants elsewhere in the swidden. The net effect would be to increase the presence of valuable species in forest regeneration during fallow succession.

Germination and establishment of valuable

Plants in managed fallows

As the swidden fades into fallow, seedling establishment of valuable plants may be enhanced over that which occurs in unmanaged fallows, due to changes in canopy structure as a consequence of management activities. The noncontinuous overstory which results from management can influence the establishment of valuable plants, because openings or 'gaps' in the canopy affects the types and diversity of species present in a stand [Denslow 1980]. In fact the distribution of gaps in the forest is one of the most important factors determining species distribution [Halle et al. 1978; Denslow 1980]. The numerous small gaps in managed fallows are places where micro-climatic conditions would favor the germination and establishment of species adapted to take advantage of gaps of this particular size. Non-valuable plants growing in these gaps would be selected against through periodic slashing. Such a situation would favor the establishment of valuable fruit trees which are usually large seeded, poorly dispersed, and need an opening for growth to reproductive size. Cousens [1965] and Poore [1968] suggest that shifts in the size frequency distribution of gaps (due to climatic fluctuations in their examples) in a given rainforest can affect the relative regeneration successes of different tree species.

Lack of seed dormancy can also play a role in the establishment of valuable plants in managed fallows. In general dormancy appears to be a characteristic of pioneer plants [Vasquez-Yanes 1974]. Opler et al. [1980] highlight that the proportion of plants with seed dormancy decreases with seral age. Thus large seeds of fallow cycle fruit trees would need to find a suitable germination site quickly in order to establish themselves. The much greater frequency of suitable germination sites in and around gaps in managed vs. unmanaged fallows would allow for more large fleshy fruits to establish themselves in managed fallows, resulting in a greater number of fruit trees later in the fallow cycle. These trees would then ideally be spared when the site is again cleared for cultivation.

Frugivore foraging strategies

The canopy structure and distribution of fruit trees in managed fallows can induce a change in the foraging activities of frugivores which visit these sites. Such a change may result in a more efficient dispersal of seeds from valuable fallow fruit trees, thus increasing the chances of seeds being dispersed to adequate germination sites. Fleming et al. [1977] note that the foraging behavior of frugivorous bats is highly responsive to the spatio-temporal differences in distribution patterns of fruit trees as Johns [1988] does for other frugivores. Because foraging operates within the constraints of an energetic balance of costs and benefits [Hamilton and Watt 1970; Schoener 1969] foraging strategies tend to optimize energetic return per unit of effort and time expended [Fleming et al. 1977]. Thus the temporal and spatial distribution of fruit trees would determine the foraging strategy used. Two different strategies are presented by Fleming et al. [1977]. When fruit trees are evenly distributed throughout the forest, the optimal strategy is to commute and search simultaneously. When food resources are clumped in patches however (as in managed fallows) the optimal strategy is to first commute to the food resource and then search for food, as there is little return from searching for food between known clumps of fruit trees [Fleming et al. 1977]. This is what Fleming et al. [1977] refer to as the 'separate strategy' (first commuting then searching). Bats which locate a reliable food source can experience a reduction in food search costs and flight times [Fleming 1981]. Thus fruit trees in managed fallows would not casually attract the frugivores necessary for dispersal, but would fit into an optimal mode of foraging behavior. The foraging strategy which is employed appears to depend not on the species of bat in question, but on the food used at a particular time [Fleming et al. 1977] and the availability of food resources. Because bats can 'switch' from one strategy to another [Fleming et al. 1977] the distribution pattern of fruit trees which is most prevalent in an area, might engage greater numbers of bats. This could in turn act to further decrease the competition for frugivores by fruit trees in managed fallows.

The chance of a seedling being in direct competition with large trees or other seedlings is reduced by dispersion [Smythe 1970]. A greater abundance of suitable establishment sites in the area of dispersion would likewise decrease this competition. Thus the potential exists for the interaction of enhanced dispersal in managed fallows, with a relatively greater number of available establishment sites in these fallows. This may result in a greater number of successful germinations and establishments of valuable fruit trees during the fallow cycle. When it then comes time to clear forest or fallow for cultivation, the presence of a greater number of fruit trees will encourage the agriculturalist to leave these valuable trees standing in his swidden, thus furthering fallow management and continuing the cyclic increase of valuable fallow plants.

Seed shadows, use of trails, flight patterns

Frugivore behavior is further influenced through the use of man-made trails as flyways. For bats, nightly movements are typically made along well travelled flyways which include man-made trails [Palmeirim and Etheridge 1985; Tuttle 1976; Fleming et al. 1977] that are especially common in areas of swidden agriculture. Posey [1985] estimated that there were approximately 500 km of trails an average of 2.5 m wide in the proximity of one of the Amazonian villages included in his study. In and around managed fallows there will be a greater number of well maintained trails (reflecting the continued use of these fallows) than in the neighborhood of unmanaged fallows. The use of man-made trails by bats during nightly foraging influences their flight patterns and effects seed dispersal because bats drop seeds while commuting [Palmeirim and Etheridge 1985]. This suggests that a bat generated seed shadow is created along man-made trails [Palmeirim and Etheridge 1985]. Janzen et al. [1976] also note the relationship between commuting routes and seed dispersal. Several studies have quantitatively described the different characteristics of frugivore generated seed shadows [Janzen 1970, 1971, 1978a, 1978b; Fleming and Heithaus 1981; Smith 1975; McDonnell and Stiles 1983]. Seed shadows are important to the reproductive success of animal dispersed plants, spatial patterning of plant communities, and selection of fruit characteristics [Thomas et al. 1988]. Fruits located relatively near trail systems have a greater exposure to the many bats using these flyways than fruit trees located far from trails [Palmeirim and Etheridge 1985]. Dispersal from near-trail fruit trees to the near-trail abundant establishment sites may further enrich the general area around managed fallows. Thomas et al. [1988] highlight the importance of the interaction between seed shadows generated by birds and bats and the availability of 'safe sites' for germination and survival of seeds.

Open swiddens in areas of managed fallows (especially those with standing fruit trees) may become part of the network of flyways in and around managed stands. This could allow these swiddens to be part of frugivore generated seed shadows, possibly enriching, at an early age, swiddens with seeds of valuable fruit trees.

Sites most frequented by frugivores for commuting, foraging, and roosting will be sites of defecation as well [Howe and Primack 1975]. And this can be an important nutrient addition to the soil [Snedaker 1980; McDonald 1971] representing a concentration of nutrients from a foraging radius of many kilometers [Snedaker 1980].

Fruit tree dispersal strategies

The type of fruit trees present in managed fallows, in particular the size and structure of the fruits themselves, can encourage particular patterns of seed dispersal. Such characteristics are known to attract specific frugivore feeding assemblages which disperse seeds in specific patterns [Pratt and Stiles 1983;

1985; Pratt 1983]. Certain patterns may help to enrich managed fallows and the surrounding forest with valuable fruit trees.

Recent studies have emphasized two different fruit tree seed dispersal strategies: large nutritious fruits consumed by 'specialized' frugivores which eat primarily fruit, and small fruits of poor quality eaten by 'opportunistic' frugivores which also frequent other food sources [Howe 1982; Pratt and Stiles 1985; Fleming 1981; Snow 1971; McKey 1975; Howe and Estabrook 1977]. Those fruit trees managed by humans in fallows would usually be of the large nutritious type. Thus one would expect that managed fallows would be visited most frequently by specialist dispersers willing to seek out the fruit they particularly favor. The type of disperser which most often frequents managed fallows will play an important role in the pattern of dispersal of managed fallow fruit tree seeds, and have an influence on the presence of fruit trees in and around managed fallows.

In a study comparing the fruit production and animal activity of different trees which attract opportunist vs. specialist dispersers, Howe [1982] found that dispersal of seeds from the tree which attracted specialist dispersers was more efficient (measured by the percentage of seed removed from under different plants) than the tree which attracted opportunist dispersers [also Howe and Primack 1975]. Waste of the 'cheap' fruits of the opportunist attracting tree was enormous. Two-thirds of the crop falls or is dropped beneath the parent trees, and only a small fraction of those seeds removed have a chance of germination and establishment [Howe 1982; Howe and Primack 1975]. Specialist frugivores on the other hand produce patterns of seed distribution and resulting seed mortality which are more beneficial to the plant [Howe and Primack 1975]. For the specialist dispersal pattern observed by Howe and Primack [1975] it was found that the distribution of seedlings between fruit trees of the same species was greater than the sum of the distributions away from the trees. In the managed fallow context, this means that specialist frugivores are more likely to disperse seeds within areas of managed fallows where more fruit trees are present. This could further favor the establishment of fruit trees in managed fallows due to the greater abundance of potential establishment sites. Depending on the species, dispersal quality can be directly related to the number of seeds deposited in light gaps [Fleming 1981].

Howe [1982] observes that the fruiting season of the opportunist tree was more sharply peaked, while the fruiting season of the specialist attracting tree was spread more evenly throughout the season (although Jackson [1981] presents evidence suggesting a correlation between large seed size and a peaked fruiting season). Such a situation in managed fallows might be to the advantage of certain species of fruit trees themselves, as competition for animal dispersal (important among large fleshy fruit species) is reduced for some species with staggered fruiting seasons [Smythe 1970]. In fact competition for dispersal itself can act as a selective influence on fruiting season [Smythe 1970; Frankie et al. 1974; Foster 1982]. And Foster [1982] has reported that fruiting season peaks and the amplitudes of peaks can actually shift from one year to the next.

The efficiency of animal dispersal is tied to the number of seeds eaten. A staggered, or longer fruiting season could encourage dispersers to frequent the area, in a sense keeping them readily available for seed dispersal; perhaps enhancing dispersal efficiency. Indeed Fleming [1981] has observed that a longer fruiting season causes reliability of visitation by specialized frugivores. And while it might be argued that a staggered or more evenly spread fruiting season might not provide enough fruits at any one time to attract many dispersers reliably, this would depend on the number of trees in the area. And, with an enhanced crop production of the specialist attracting tree, due to the reduction in competition and availability of nutrients via management practices, frugivores might be encouraged to further 'camp out' on the resource, depositing seeds nearby [Howe 1982; Heithaus and Fleming 1978]. While the possibility exists for all this local dispersal to overwhelm the potential establishment sites in managed fallows, it is not likely because a substantial number of fruits would be harvested by the farmers who are managing the fallows.

Changes in fallow species' abundance, composition and distribution as well as spatial changes in fallow vegetation due to plant management, could take advantage of the latent habits of frugivores. That characteristics of fruits and the number and distribution of fruit trees do influence the behavior of frugivorous species appears to be widely observed [Wheelwright 1983; Beehler 1983; Snow 1962, 1971; McDiarmid et al. 1977; Howe 1977, 1981; Ricklefs 1977; Leck 1971; Fleming 1981].

Prehistoric evidence and present day examples

Plant management in the past can affect the present day geographic distribution or population parameters of the species being manipulated. The literature designates as 'relict' a plant species whose distribution and density at the present time has resulted from some past human manipulation in a specific region [Turner and Miksicek 1984]. In fact researchers have cautioned botanists against considering tropical forests as virgin, undisturbed, or primary because the effects of past human activities may continue to be evident long after the population responsible has disappeared [Posey

1985; Alcorn 1981]. Numerous investigations have indicated that the present day distribution and composition of useful species in forests near Mayan sites may reflect previous forest management [Barrera et al. 1977; Folan et al. 1979; Lundell 1933, 1937, 1938; Puleston, 1968, 1978; Netting 1977; Cook, 1909; Gordon 1969, 1982]. Alcorn [1981] observes similar forest manipulation continuing from prehistoric times in northern Mexico. And several authors have presented evidence attesting to the existence of large populations in prehistoric Amazonia [Denevan 1976; Lathrap 1970; Smith 1980; Nimuendaju 1939; Ribeiro 1976; Neel 1970; Arnaud and Alves 1974] which very likely were engaged in forest management [Denevan et al. 1984; Posey 1985].

The arguments against relict plant populations are summarized by Turner and Miksicek [1984] and focus on the lack of a strong statistical correlation between certain plant species and elite Mayan residences, and the observation that some relict economic species of the Maya are commonly found in plots of long fallow. However after centuries of seed dispersal, it should not be surprising that there is not a tight correlation between the present distribution of certain economic species and precise locations of prehistoric sites. Both Posey [1985] and Alcorn [1981] mention the long term growth and movement of managed or 'anthropogenic' vegetation zones. That many economic species said to have been used by the Maya are secondary successional species presently found in long fallow plots would seem to be evidence that some economic species, having gained a foothold in an area due to human manipulation, i.e., a high frequency of secondary sites, are able – via ecological processes – to continue a significant presence in the area in association with swidden agriculture. Such secondary species may very well continue to thrive in fallow plots of the proper successional stage in old Mayan areas of continual occupation by swidden agriculturalists.

That the Maya were able to successfully manage forests reflects their ecological knowledge. The Maya appear to have had specific practices of conservation, modification and multiple use of the forest, as well as a knowledge of successional changes in vegetation [Barrera et al. 1977] and taxonomy [Barrera et al. 1976].

Additional evidence exists supporting the premise that prehistoric societies did manage trees and forests. Turner and Miksicek [1984] mention Spanish accounts of post-classic Maya orchards near settlements, as well as seed, stem and wood fragments and pollen data to identify both wild and domesticated fruit trees used by the Maya. This suggests pre-historic use of orchard gardens similar to those observed in Mayan areas today [Netting 1977]. Linguistic evidence for use of economic species, including tree species, is presented for the Maya by McQuowan [1964]. And species identification, including fruit trees, using Mayan iconography has also been suggested [Schele 1978; Thompson 1981].

Similar examples

Similar examples of a spontaneous increase in economic species include the case of the west African oil palm (*Elaeis guineensis*). Occurring naturally on the edges of forests the oil palm has become concentrated in areas under frequent swidden cultivation where high forest has been reduced to bush. As the farmers clear the land in preparation for cultivation, the oil palm is spared. As a result, stands of the palm have become thicker and thicker over the years. In some areas large stands of oil palm have developed without a seed ever having been planted [Harlan 1975]. Another example is that of karite (*Butyrospermum* spp.). In this case the tree is not valuable economically, rather the protection is the result of the tree's status as a semi-sacred plant. Nevertheless the result is that almost pure stands of karite trees inhabit large areas of the West African broadleaved savanna [Harlan 1975]. While these examples do not take place in humid tropical forests where ecological processes are more complex, they do point out the long-term value of sparing valuable trees.

Conclusions

The increase in the number of valuable plants in managed fallows with each successive fallow cycle would depend to a considerable degree on the favored germination and establishment of these plants in the managed fallow. Seed of parent trees which were left uncut in the swidden may have a greater chance of surviving a burn, and would, below the parent tree, have greater access to nutrients for longer periods of time than regrowth plants elsewhere in the swidden. As the site is slowly abandoned and the fallow cycle is initiated, the germination and establishment of valuable plants would continue to be favored. The interaction between managed fallow canopy structure, and the composition, abundance, distribution, and dispersal strategies of valuable fallow plants (especially fruit trees), together with the foraging behavior of frugivores, has the potential to greatly increase the number of successful establishments of seedlings of valuable plants in managed fallows.

The applied implications of the ecological evidence presented would seem to be that certain economic species are able to take advantage of the ecological processes which occur in conjunction with managed swidden fallows to successfully survive and increase their numbers over the long term. The agroforestry approach taken toward this form of fallow utilization therefore should include management techniques which encourage the ecological processes which are important in promoting a spontaneous presence of economic species. Such techniques would likewise be useful in the promotion of man-made community enrichment as well.

The presence of a greater number of valuable perennial plants in areas under swidden agriculture would encourage the management of a greater number of fallows. When the farmer decides to manage a fallow or not, the presence of valuable trees in the fallow about to be cleared is of primary importance. The farmer will be encouraged to manage the fallow if there are already a number of valuable species in it, thus further contributing to the regional spontaneous increase in economic plants.

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