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REVIEW

The ecological implications of harvesting non-timber forest products

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Summary

1. The harvest of wild non-timber forest products (NTFP) represents an important source of income to millions of people world-wide. Despite growing concern over the conservation of these species, as well as their potential to foster forest conservation, information on the ecological implications of harvest is available only in disparate case studies.
2. Seventy studies that quantify the ecological effects of harvesting NTFP from plant species were reviewed, with the aims of assessing the current state of knowledge and drawing lessons that can provide guidelines for management as well as better directing future ecological research in this area.
3. The case studies illustrated that NTFP harvest can affect ecological processes at many levels, from individual and population to community and ecosystem. However, the majority of research was focused at a population level and on a limited subset of plant parts that are harvested.
4. Tolerance to harvest varies according to life history and the part of plant that is harvested. Moreover, the effects of harvest for any one species are mediated by variation in environmental conditions over space and time, and by human management practices.
5. In order to withstand heavy harvest, specific management practices in addition to gathering are necessary for many NTFP species. Management practices can be carried out at different spatial scales and some are highly effective in fostering population persistence.
6. *Synthesis and applications*. Substantial advances have been made towards identifying the ecological impacts of NTFP harvest. However, there is a need for longer-term studies that focus on multiple ecological levels (ranging from genes to ecosystems), that assess the mechanisms underlying impacts and that validate current models. Researchers and forest managers need to work with local harvesters in designing and evaluating management practices that can mitigate the negative effects of harvest.

Key-words: conservation, extraction, harvest, matrix models, non-timber forest products, resource management, review, sustainable development.

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Introduction

Non-timber forest products (NTFP) have been harvested by human populations for subsistence use and trade over thousands of years. Over the past two decades, NTFP obtained from plant resources, including seeds, flowers, fruits, leaves, roots, bark, latex, resins and other non-wood plant parts, have gained much attention in conservation circles. The growing commercial trade of natural products, in particular plant medicines and crafts, has resulted in the harvest of increasing volumes from wild plant populations (Kuipers 1997; Lange 1998) and has therefore generated concern about overexploitation (Rebelo & Holmes 1988; Vásquez & Gentry 1989; Cunningham 1993; Clay 1997; Rawat 1997; Tiwari 2000). For instance, of the 1543 medicinal plant species traded in Germany, 93–98% are harvested from wild populations (Lange & Schippmann 1997). Similarly, more than 95% of the 400 plant species used in the production of medicine by the Indian herbal

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Table 1. Focus of studies that quantitatively assess the ecological implications of harvesting non-timber forest products

Level	Type of assessment	Number of studies
Individuals	Rates of growth, survival and reproduction	16
Populations and individuals*	Population structure and dynamics	42
Communities	Community structure and composition, plant–animal and plant–plant interactions	9
Ecosystems	Nutrient and organic matter dynamics, energy exchange	3
Total		70

*Includes papers that assessed the effects of harvest on plant populations only, as well as those that assess the effects of harvest on both individuals and populations.

industry are harvested from wild populations (Uniyal, Uniyal & Jain 2000). It is estimated that between 4000 and 6000 non-timber plant species are of commercial importance world-wide (Iqbal 1993; SCBD 2001).

Furthermore, hundreds of millions of people worldwide currently derive a significant portion of their subsistence needs and income from gathered plant and animal products (Iqbal 1993; Walter 2001). Moreover, those people who are most economically dependent on these resources tend to be the poorest members of the community. Sustainable harvesting is therefore not only essential for conservation of the plant species, but also for the livelihoods of many rural peoples. Indeed, promotion of the commercial extraction of NTFP as a conservation strategy is based on the argument that forest conservation must be able to offer economic incentives to local rural peoples in order to counter the threat from destructive land uses such as logging and cattle ranching. This strategy has gained wide acceptance as a conservation paradigm (Nepstad & Schwartzman 1992; Panayotou & Ashton 1992; Plotkin & Famolare 1992).

The social, economic and political conditions necessary for sustainable extraction of NTFP have been debated widely (Parks, Barbier & Burgess 1998; Kline, Alig & Johnson 2000; Shackleton 2001; Amacher 2002) and the greatest barriers to sustainable harvesting may fall within these domains. However, at the heart of this issue, and of the many agreements and policies at both national and international levels that relate to management of NTFP, there lies a fundamentally important ecological question: what are the ecological consequences of NTFP harvest? Although it is very often assumed that harvest of NTFP has little or no ecological impact, extraction of non-timber plant parts may alter biological processes at many levels. For instance, harvest may affect the physiology and vital rates of individuals, change demographic and genetic patterns of populations, and alter community- and ecosystem-level processes.

Research on the ecological consequences of NTFP harvest has been growing rapidly over the past two decades, but the information is contained in disparate case studies. In this paper, the results of 70 studies that assess the ecological effects of NTFP harvest are reviewed. These papers were obtained from extensive searches in *Biological Abstracts* and *BioOne* databases and were selected because they met two criteria: (i) they presented quantitative, empirical ecological analyses that specifically assessed the effects of NTFP harvest; and (ii) they focused on NTFP derived from plants that are primarily wild-harvested, although some may be cultivated on a small scale. The consequences of harvest at different ecological levels are presented, from individual to ecosystem, and the sources of variation that influence the effects of harvest are emphasized. Based on the results, some recommendations for NTFP management are made and future research priorities are outlined. The aims of this paper are to assess the current state of knowledge in this area and draw lessons from the case studies that could (i) provide guidelines for resource managers; (ii) help policy makers, conservation organizations, foundations and others make informed decisions on the management and/or promotion of these plant products; and (iii) better direct future ecological research in this area. Note that although many of the 70 papers are highlighted in order to emphasize and illustrate certain points, not all them appear explicitly in the text or references cited.

Effects of harvest on plant individuals and populations

The most direct ecological consequence of NTFP extraction is alteration of the rates of survival, growth and reproduction of harvested individuals. Changes in these vital rates can, in turn, affect the structure and dynamics of populations. More than three-quarters of the ecological research on NTFP was focused at the level of individuals and populations (Table 1). Because sustainability of resource use requires, at the very least, that harvest rates do not exceed the capacity of populations to replace the individuals extracted (Hall & Bawa 1993), many of the studies have attempted to derive harvest limits based on demographic data (Table 2). The studies illustrate that the effects of harvest on both individuals and populations are highly variable and are mediated by different sources of variation.

VARIATION IN PLANT PART AND LIFE HISTORY

When a portion of plant material is harvested from an individual, the nature and quantity of nutrients and/or

Table 2. Annual maximum sustainable harvest limits proposed for non-timber forest products, based on demographic analyses

Part harvested*	Species	Life history†	Environment‡	Annual sustainable harvest rate (%)	Method used to obtain rate§	Reference
Seeds/fruits	*Phytelephas seemanii*	Palm, U	TE	86	MU	Bernal (1998)
	Neodypsis decaryi	Palm, C	TE	95	MU	Ratsirarson, Silander & Richard (1996)
	Brosiumum alicastrum	Tree, C	TE	95	MU	Peters (1992)
	Grias peruviana	Tree, U	TE	80	MU	Peters (1991)
	Berthollia excelsa	Tree, C	TE	*c.* 93¶	MH	Zuidema & Boot (2002)
Leaves	*Neodypsis decaryi*	Palm, C	TE	25	MU	Ratsirarson, Silander & Richard (1996)
	Livingstonia rotunidifolia	Palm, U	TE	< 20	VE	O'Brien & Kinnaird (1996)
	Geonoma deversa	Palm, U	TE	All leaves on 8–16 year rotation	MH	Zuidema (2000)
	Aechmea magdalenae	Herb	TE	75	MH	Ticktin *et al.* (2002)
	Rumohra adiantiformis	Fern	ME	50	VE	Geldenhuys & Van der Merwe (1988)
	Mattecuia struthiopteris	Fern	TD	< 50	VE	Bergeron & Lapointe (2000)
Inflorescence	*Banksia hookeriana*	Shrub	H	*c.* 20 (once established after fire)	VE	Witkowski, Lamont & Obbens (1994)
Whole plants	*Allium tricoccum*	Herb	TD	0–16	MU	Nault & Gagnon (1993); Nantel, Gagnon & Nault (1996)
	Panax quinquefolium	Herb	TD	5–15	MU	Charron & Gagnon (1991); Nantel, Gagnon & Nault (1996)
	Hydrastis canadensis	Herb	TD	< 10	MH	D. Christensen & D. Gorchov, unpublished data
	Aechmea magdalenae	Herb	TE	35	MH	Ticktin *et al.* (2002)
	Prunus africanus[a]	Tree, C	TE	0 (on 8–10 year rotation)	MH	Stewart (2001)
	Aquilaria malaccensis[b]	Tree, C	TE	> 10 cm d.b.h.	MU	Soehartono & Newton (2001)
	Aquilaria microcarpa[b]	Tree, C	TE	0 (> 30 cm d.b.h. every 15 year)	MU	Soehartono & Newton (2001)
	Thrinax radiata[c]	Palm, C	TSE	40 ha^{-1}	MU	Olmsted & Alvarez-Buylla (1995)
	Coccothrinax readii[c]	Palm, C	TSE	0	MU	Olmsted & Alvarez-Buylla (1995)
	Euterpe precatoria[d]	Palm, SC	TE	0	MU	Zuidema (2000)

*Whole plants harvested for [a]bark; [b]resin in wood; [c]leaves and wood; [d]apical meristem.

†U, understorey; C, canopy; SC, subcanopy species.

‡TE, tropical evergreen forest; TSE, tropical semi-evergreen forest; TD, temperate deciduous forest; ME, montane evergreen forest; H, heathland.

§Demographic method by which maximum annual sustainable harvest rate was obtained: MU, matrix model projections based on simulations of unharvested populations; MH, matrix model projections based on simulations of harvested populations; VE, effects of experimental harvest on vital rates.

¶Maximum sustainable harvest rate was not estimated but populations harvested at this level were found to be stable.

d.b.h., diameter at breast height.

photosynthetic capacity removed, and the potential for survival and effective propagation, will depend on the kind of material harvested. It is not surprising then, that the type of plant part harvested affects the potential for species to tolerate harvest (Table 2). For instance, within a life-history form such as trees, estimated harvest limits for seeds or fruits are much higher than those for leaves. The data also suggest that many trees are not able to withstand even the lowest rates of harvest when harvest leads to mortality of the individual. (Note that the harvest of NTFP such as stems, bark and apical meristems can imply harvest of whole trees). In contrast, very high levels of fruit or seed harvest of some trees may actually permit population persistence over the long term (but see the effects on community discussed below). However, this excludes seed or fruit harvesting that also involves damage to other parts of the trees, which often occurs during fruit harvest (Vasquez & Gentry 1989; Sinha & Bawa 2002).

Tolerance to harvest also varies with life history. For example, populations of perennial herbs can withstand higher rates of harvest than populations of trees, the latter tending to be much slower growing and longer lived (Table 2). These data are supported by matrix model elasticity analyses of the tree species studied, which indicate that survival of the largest stage classes contribute most to population growth while seed survival contributes very little (Peters 1991, 1992; Olmsted & Alvarez-Buylla 1995; Joyal 1996; Ratsirarson, Silander & Richard 1996; Bernal 1998; Zuidema 2000; Stewart 2001).

It is noteworthy that although NTFP are extracted from an enormous variety of plant species (FAO 1995), the majority of research at individual and population levels has concentrated on a limited number of life forms and plant parts (Table 3). Nearly 40% of the studies focused on palms, but few studies have addressed lianas or vines. About half of the research examined the effects of harvest of fruits/seeds and leaves. Although plant exudates such as gums, resins and oleoresins, as well as barks, roots and bulbs, represent a large proportion of commercial wild-harvested NTFP (Cunningham 1993; Vantomme, Markkula & Leslie 2002), the ecological consequences of harvesting these plant parts remain poorly studied.

VARIATION IN ENVIRONMENTAL CONDITIONS

Tolerance to harvest varies with climatic conditions, in particular with the resources available to stimulate plant growth and recuperation after harvest. For instance, all the temperate herbs studied were perennial and appear to be highly vulnerable to harvest of individuals (Table 2). This is in contrast to the only tropical perennial herb studied, *Aechmea magdalenae*, which can tolerate higher levels of harvest. Unlike the temperate herbs, *A. magdalenae* enjoys a year-round growing season.

Similarly, none of the understorey palms appears to be able to tolerate high levels of leaf harvest (Zuidema 2000; Svenning & Macia 2002; Endress *et al.*, in press; F. Ramirez, unpublished data), at least in primary forest conditions. In contrast, several of the canopy and open-environment palms can withstand much higher rates of leaf harvest (Fong 1995; Joyal 1996; Ratsirarson, Silander & Richard 1996). While this data set is small, it suggests that light availability may be a limiting factor for some understorey species.

Rates of growth and demographic responses to harvest may also vary significantly over climatic or soil gradients (Shankar *et al*. 1996; Siebert 2000; Paoli *et al*. 2001; Svenning 2002). Similarly, the demographic behaviour of populations varies over time as environmental conditions change (Menges 2000). Stochastic models of harvested populations illustrate that the responses of some species to harvest varies significantly over years with different environmental conditions (Nantel, Gagnon & Nault 1996), while others vary little despite great variation in environmental conditions (Ticktin *et al*. 2002). Identification of those attributes that may allow species to have more consistent responses to harvest over temporally varying environmental conditions could provide insight on which species may be best able to persist over the long term.

Environmental variation presents a challenge to our current understanding of ecological impacts of NTFP extraction. The average number of populations per study reviewed was fewer than three, and the mode was only one. Similarly, more than two-thirds of the studies had a duration of 2 years or less, and only about 10% monitored populations for more than 3 years.

Table 3. Number of non-timber forest products for which the effects of harvest have been quantitatively assessed, according to life form and part of plant harvested

	Palms	Trees and shrubs	Herbs	Vines or lianas	Bryophytes	Total
Flowers		3	4			7
Fruits/seeds	5	9				14
Leaves	16		6			22
Roots, bulbs, corms			3	2		5
Branches		1				1
Bark		2				2
Resin		3				3
Apical meristem, stems or whole plant	7		5		2	11
Total	28	18	18	2	2	68

Clearly, longer term studies over variable environments are necessary.

VARIATION DUE TO MANAGEMENT

The impacts of variation in life history, plant parts and environment on harvest limits and capacity for regeneration support some previous hypotheses and guidelines for assessing which NTFP have the most potential to support livelihoods and foster conservation (Peters 1994; Cunningham 2001). Other characteristics are also expected to influence tolerance to harvest, including reproductive strategy, habitat specificity and growth rates. However, the data also illustrate the great variability in tolerance to harvest, even among species that share similar life histories, harvest types and environments. This variability can be due, at least in part, to variation in management by people.

The term 'management' is used here to encompass a range of management practices that are carried out at differing spatial scales. At one level are harvest-specific practices: the specific methods by which the target plant parts are extracted from individual plants. A second level includes additional management practices carried out on either the harvested or surrounding plants and animals that aim to enhance production. Management at this level can include pruning, weeding, sparing, fertilization and planting seeds or vegetative propagules (Casas *et al*. 1996). A third level of management refers to other uses for the land on which the NTFP resources grow, e.g. logging, cattle ranching, agriculture and other activities that set the context in which NTFP harvesting occurs. The ways in which the ecological effects of NTFP harvesting are strongly mediated by management at these three levels are reviewed below. The management options open to local people are highly dependent on systems of land tenure and governance, socio-economic status, population pressure, education, government policies as well as cultural factors. The relationships between these factors and NTFP management practices have been discussed in depth elsewhere (Cunningham 1993; FAO 1995).

VARIATION IN HARVEST METHOD

The majority of research at the level of individuals has focused on experimental assessments of harvest methods, and clearly illustrates that vital rates of non-timber resources may be significantly affected by differences in harvest techniques. These include seasonal timing of harvest, timing of harvest in the plant life cycle, frequency of harvest, size of individuals harvested and intensity of harvest (Geldenhuys & Van der Merwe 1988; Nantel, Gagnon & Nault 1996; Anderson & Rowney 1999; Zuidema 2000; Ticktin *et al*. 2002; Freckleton *et al*. 2003; Endress *et al.*, in press). In addition, the intensity of harvest may vary over time due to changing socio-economic circumstances. Harvest simulations based on stochastic matrix projection models, which involve the random alternation of a series of different yearly matrices, illustrate that different sequences of annual variations in harvest intensity can have significant impacts on population growth rates (Nantel, Gagnon & Nault 1996; Stewart 2001). The way in which the plant is cut to obtain the desired product can also result in differences in population growth rates (Flores & Ashton 2000; Ticktin & Johns 2002). Variation in spatial patterns of harvest may also have lead to significant differences in rates of growth and reproduction (T. Ticktin, unpublished data).

The diversity of methodologies and management techniques used in experimental harvests makes comparisons among species very difficult and points to the need to standardize methodologies. Moreover, most studies are limited by their short time frames (more than 95% of the study time frames were between 1 and 3 years). For instance, all six studies that assessed partial defoliation of palm species showed that leaf harvest can result in increased or equal levels of growth and reproduction (Mendoza, Pinero & Sarukhan. 1987; Chazdon 1991; Oyama & Mendoza 1990; Fong 1995; Ratsirarson, Silander & Richard 1996; Endress *et al.*, in press). However, ecophysiological studies have illustrated that some species can allocate resources to growth and reproduction after defoliation through reallocation of stored reserves (Whitham *et al*. 1991). This could allow for higher rates of growth in the short term but not necessarily over the long term. Defoliation may also alter carbon (C) content, carbon : nitrogen (C : N) ratios and chlorophyll content in new leaves, making them more susceptible to herbivores and decreasing photosynthetic capacity over the long term (O'Hara 1999). Clearly, ecophysiological studies will be an important compliment to experimental harvests if the latter are used as tools for assessing the potential long-term effects of different management practices.

One shortcoming of research on experimental harvests is that few of the studies have simulated management practices actually used by local people. Given that local management practices are usually based on both ecological as well as cultural and socio-economic considerations, proposals for changes in management such as timing or frequency of harvest may be impractical or impossible for local harvesters. A more useful approach would be to focus on assessing harvest practices currently employed by local peoples or adaptations of those currently used by local people.

VARIATION IN ADDITIONAL MANAGEMENT PRACTICES

The effects of some NTFP harvest techniques may be enhanced or exacerbated by the use of additional management techniques. A small but growing number of studies has quantitatively illustrated that certain management practices can maintain or increase individual

Table 4. Management practices that can promote population persistence of specific non-timber forest products

Management practice	Reference
Sparing of individuals	Joyal (1996)
Size restrictions	Nantel, Gagnon & Nault (1996); Joyal (1996); Svenning & Macia (2002)
Overstorey light management	Ticktin & Johns (2002)
Thinning	Ticktin & Johns (2002)
Transplanting	Ticktin & Johns (2002)
Coppicing	Anderson (1991)
Replanting plant parts (seeds or vegetative parts)	Anderson & Rowney (1999); Martinez-Ballesté *et al*. (2002)

and population growth rates (Table 4). Some management practices, such as thinning of dense populations or sowing of seeds, may actually result in growth rates of harvested populations that exceed those of non-harvested populations (Martinez-Ballesté *et al*. 2002; Ticktin *et al*. 2002). Moreover, the effects of these management practices may interact with harvest techniques in different ways. For example, the fibrous leaves of the bromeliad *Aechmea magdalenae* can be harvested by cutting only the longest leaves or by cutting the whole plant to obtain the leaves (Ticktin & Johns 2002). Cutting the whole plant is much easier and less time consuming. Demographic models of harvested populations illustrate that populations subject to the leaf harvest method provide higher fibre yields and grow faster than those subject to the plant-harvest method. However, when additional management practices, such as light management and thinning, are carried out the exact reverse is found to be true. These additional management practices were developed by people who have been harvesting this species for hundreds of years (Ticktin & Johns 2002; Ticktin *et al*. 2002).

At the same time, many harvest and management practices can also greatly exacerbate the negative effects of harvest. For instance, although model simulations of high levels of fruit harvest indicate that this may be sustainable in some species (Table 2), in reality destructive fruit-harvesting techniques such as branch cutting have led to the decline of many species (Vasquez & Gentry 1989; Cunningham 1993; Sinha & Bawa 2002).

VARIATION IN LAND-USE CONTEXT

Populations of non-timber species growing in landscapes subject to different kinds and levels of anthropogenic pressure may respond to harvest in very different ways. Several understorey NTFP are able to withstand higher harvest levels and have greater capacities for regeneration in secondary forests than in primary forests, due to the higher light availability in the former (Siebert 2000; Svenning 2002; Ticktin, Johns & Chapol Xoca 2003; F. Ramirez, unpublished data). Frequency, intensity and time since burning can also have a significant impact on rates of growth of NTFP (Sinha 2000; Plowden, Uhl & Oliveira 2003). Despite the fact that non-timber species are often harvested in conjunction with logging operations, there exists little ecological data on how these types of extraction interact (Salick, Mejia & Anderson 1995; C. Plowden, unpublished data).

Rates of growth and reproduction of NTFP growing in agroforestry systems, enhancement forest plantings and home gardens may also differ significantly from those in unmanaged forest environments, due to differences in intraspecific competition (Ticktin, Johns & Chapol Xoca 2003), light (Velasquez-Runk 1998) or a combination of factors (Martinez-Ballesté *et al*. 2002).

Despite the important role that management appears to play in influencing the dynamics of harvested populations, this aspect has been overlooked by many studies. Of the 24 studies that used matrix projection models to assess the effects of harvest on rates of population growth, only about half were based on harvested populations. The others simulated harvest using demographic parameters obtained from monitoring unharvested populations, and assumed that the only demographic consequences of harvest would be increased mortality of the stage class harvested (for instance increased mortality of seeds or adults). However, NTFP harvest may provoke significant changes to rates of growth, reproduction and survival of individuals in a range of stage classes that are not subject to harvest. Empirical comparisons of harvested and non-harvested populations suggest that, at least for some species, simulations of harvest using models of unharvested populations may provide highly misleading results (Ticktin *et al*. 2002). This may be especially true in the case of species showing density dependence, where density-dependant and density-independent simulations of harvest can produce very different results (Price 1999; Freckleton *et al*. 2003). The fact that about half of all the species from the papers reviewed grow in dense stands or clumps points to the need to assess empirically the dynamics of harvested populations and to analyse the management practices to which they are subject.

Effects of NTFP management on ecological communities

Although most studies of NTFP have been focused at the population level, long-term population persistence by no means implies that harvest does not have major negative effects on other members of the ecological community. The few studies that have investigated the effects of NTFP harvest on communities or ecosystems (Table 1) suggest that ecological impacts at these levels may also be significant.

The majority of forest fruits collected for sale are those eaten by large mammals and birds (Hladik, Leigh & Bourliere 1993), but the effects of fruit, seed or flower harvest on frugivores and granivores remain largely unknown. One study suggests that high levels of NTFP harvest and enhancement plantings may alter the composition and diversity of bird populations. Moegenburg & Levey (2002) illustrated that high-intensity fruit harvest of acai palms *Euterpe oleracea* in the Brazilian Amazon reduces avian frugivore diversity. However, low-intensity harvest has no effect. The authors also show that enhancement of acai populations can support more fruit-eating birds but changes the composition of the avian community towards fruit eaters. Galetti & Aleixo (1998) illustrated that harvest of *Euterpe edulis* palm hearts negatively affected the abundance of two of 15 large frugivorous birds known to eat *E. edulis* fruits. Although primates are important seed dispersers and predators, and compete with human harvesters for food (Kinnaird 1992), the effect of fruit harvest on primates remains untested (Chapman & Onderdonk 1998).

Harvest of NTFP can also increase susceptibility of harvested plants to herbivory by insects, at least for several *Protea* species in the South African Fynbos (Mustart & Cowling 1992). In some cases NTFP production is dependent upon the activity of insects or fungi. For example, gaharu wood is produced from the resin formed due to the infection of a fungal pathogen. Although the pathology is not fully understood, wood-boring insects and ants are thought be vectors of the fungal pathogen(s) (Paoli *et al*. 2001). Similarly, the production of resin flow from several *Protium* species is stimulated by weevil larvae (Plowden, Uhl & Oliveira 2002). Although harvest and management of NTFP can be expected to have effects on pollinator populations, this remains largely unexplored.

The effects of harvest may be mediated by plant–plant interactions. For instance, hemi-parasite loads have a negative effect on fruit production of amla trees (Sinha & Bawa 2002) and therefore affect the capacity of populations to withstand fruit harvest. The ways in which spatial variation in plant–animal and plant–plant interactions mediates the effects of harvest remain untested. Anecdotal evidence, however, suggests these relationships may be significant. For instance, lower herbivore populations closer to village sites due to hunting may allow for higher rates of harvest of plants that provide herbivore food. In this sense, those plants subject to harvesting patterns that mimic biotic interactions for which they have developed evolutionary responses, such as resprouting (Siebert 2000; Ticktin 2003), may be most tolerant to harvest. This is most likely if the intensity of the biotic interaction is reduced in human-impacted areas.

NTFP harvest can alter forest structure, composition and regeneration. Bark ringing of trees in South Africa causes the formation of canopy gaps, changing forest structure and allowing an influx of invasive species (Cunningham 1993). Similarly, areas of dry deciduous forest in India that are subject to high-intensity NTFP harvest have lower species richness, basal area and tree mortality, as well as lower numbers of individuals in the smaller size classes, than comparable areas of forest with lower intensity NTFP harvest (Murali *et al*. 1996). These forests also have higher proportions of wind-dispersed vs. animal-dispersed understorey plants and seedlings, suggesting changes in species composition over the long term (Ganeshaiah *et al*. 1998). In scrub forests of the same region, Shankar, Hedge & Bawa (1998) illustrated that intensive NTFP harvesting appears to lead to replacement of large woody species by small woody species, declines in stand density and basal area, and skewing of populations towards smaller size classes. Moreover, the authors hypothesize that anthropogenic pressure may have led to the creation of scrub forest from dry deciduous forest. While forest plantations or enhancements of native wild populations can increase production of NTFP, take pressure off wild populations and make production more economically efficient, their impact on community- or ecosystem-level processes remain largely unknown.

Effects of NTFP management on ecosystems

The role that NTFP play in cycling nutrients and therefore the effects of extraction on nutrient dynamics have been quantified in a few studies (Table 1). The extent to which nutrient cycling may be altered varies with the intensity of harvest and with the plant part harvested. Long-term picking of blooms of *Banksia hookeriana* in nutrient-poor soils of Australian heathlands depletes nutrient levels of individual plants and may affect nutrient cycling at the ecosystem level (Witkowski & Lamont 1996). One problem is that the nutrient-rich leaves are harvested along with the blooms. In contrast, rattan *Calamus zollingeri* harvesting in the tropical rainforests of Sulawesi does not appear to affect nutrient cycling, as nutrients levels are significantly higher in the foliage than the cane and the foliage is left on the ground after harvesting (Siebert 2001). These studies point to the important role that nutrient cycling research can play in identifying management practices that can minimize nutrient losses.

Both temporal and spatial variation in environmental conditions can influence the effects of harvesting on nutrient cycling. O'Hara (1999) illustrated that harvesting the leaves of the palm *Sabal mauritiiformis* in Belize does not remove significant levels of limiting nutrients from harvest sites. However, she demonstrated that *S. mauritiiformis* appears to contribute significant sources of phosphorus (P), potassium (K) and zinc (Zn) sources during certain seasons and that the magnitude of the contributions of *S. mauritiiformis* to total ecosystem cycling is much greater for dense populations than for sparse populations. These results suggest that although harvesting high-density NTFP populations may be least damaging from a population perspective, it could be highly damaging from an ecosystem perspective if harvest results in the removal of important contributions to ecosystem cycling. This highlights the need for NTFP research to address a range of scales, from individual to landscape, for comprehensive ecological understanding.

Harvest of some NTFP can also exacerbate soil erosion processes. For instance, *Aloe vera* and *Asparagus racemosus* act as good soil binders in the Indian forests in which they are found, and heavy harvest of their underground portions has led to large-scale soil erosion (Ramakrishnappa 2002).

Recommendations for management and conservation of NTFP

To manage and conserve NTFP populations effectively, at least three main ecological questions must be addressed (in addition to socio-economic and political issues). (i) What are the ecological impacts of harvest? (ii) What are the mechanisms underlying these impacts? (iii) What kinds of management practices may mitigate negative impacts and/or promote positive impacts? The latter can only be answered by addressing the former questions.

This review illustrates that we have made much headway in addressing the first of these questions. It is clear that the harvest of NTFP can affect ecological processes, from the level of the individual to the ecosystem, and that the effects for any one species can vary greatly over space and time, and according to human management practices.

It is also clear that many NTFP are currently overharvested. This is evidenced by the low harvest limits presented by many of the reviewed studies (Table 2) combined with the fact that the majority of population-level studies reviewed in this paper concluded that current harvest levels appear to be unsustainable over the long-term. This suggests that many NTFP will require some kind of management if they are to withstand heavy harvest pressure.

Although each NTFP system is different, the ways in which variation in life history, plant part harvested and environment alter the effects of harvest suggest that certain management techniques might be effective in lessening the negative impacts of harvesting some types of NTFP. For instance, for those understorey NTFP that are better able to withstand harvest in higher light environments, enrichment in secondary forests, production in conjunction with logging operations and careful pruning of overstorey trees may be options for increasing the potential for sustainability. Similarly, the very low rates of adult harvest tolerated by all the trees and perennial temperate herbs reviewed here (Table 2) suggest that the development of methods to extract products such as bark, latex, resins or even fruit that lead to lower adult mortality should be a priority for NTFP management. If adult mortality is a necessary part of harvest, the maintenance of regeneration pathways, through practices such as seedling protection, maintenance of adequate conditions for germination and growth, planting and cultivation, may be required for long-term sustained production.

The ways in which the responses to harvest of some NTFP vary significantly over space and time also suggest that, at least in these cases, harvest limits may have little meaning outside the specific conditions in which they were determined. Therefore adaptive management strategies, in which harvesters are actively involved in monitoring both harvest and feedback, may be important tools for regulating harvest.

It is important to emphasize that the studies reviewed here also illustrate the diversity of human practices currently used to manage NTFP, and moreover that managed populations of at least some NTFP appear to permit long-term population persistence (Joyal 1996; Martinez-Ballesté *et al*. 2002; Ticktin & Johns 2002). Detailed knowledge of plant ecology and highly developed management practices are often found among individuals and communities who have been interacting with plant species over long periods of time (Gadgil, Berkes & Folke 1993). Populations managed by knowledgeable harvesters may show high growth rates under high harvest pressure, while populations of the same species managed by less knowledgeable harvesters may decline under much lower levels of harvest (Ticktin & Johns 2002). The promotion and monitoring of local experimentation in management techniques, through participatory research with harvesters, may therefore be one of the most important keys to identifying harvest practices that promote persistence.

Finally, the data illustrate that management options should not only focus on population persistence, but also consider the potential effects of harvest on community- and ecosystem-level processes. This could take the form of promoting simple, but additional, management practices that could accompany harvest or cultivation. For instance, management practices could include the protection, sparing and planting of seedlings of important overstorey canopy trees that might be trampled due to heavy harvesting or that might be weeded in cultivated plots; the return of non-used portions of harvested material to the forest floor to reduce nutrients removed from the system; and the planting or protection of important food plants for animal competitors.

Research priorities

Although there is growing interest in the cultivation of some NTFP, the majority will probably continue to be harvested in the wild to some extent in the foreseeable future. Although we have made advances in assessing the ecological implications of harvest, there is clearly a dearth of information available on the harvest of certain plant parts that hold great economic value, such as resins and exudates, and underground plant parts such as tubers, roots and corms. The short-term nature of most studies reviewed points to the need for much more long-term monitoring. This will be essential if we wish to consider the effects of potentially important factors such as episodic recruitment, periodic disturbances (such as fire and logging), seed dormancy and variable harvest intensity.

Similarly, the heavy focus of recent studies on the effects of harvest on individuals and populations suggests that more attention should be directed towards assessing the effects of harvest on community- and ecosystem-level processes, and assessing the effects of harvest concurrently on different ecological levels. Sustainability at one level may or may not coincide with sustainability at another level. In addition, very few studies have assessed the effects of harvest on genetic structure and diversity of harvested populations (Shaankar, Ganeshaiah & Nageswara 2001). Considering that the health of many cultivated NTFP also depends on the use of genes from wild populations (Reis 1995), this information will inevitably be necessary for designing plans for long-term sustainability.

We have little information to date on the mechanisms underlying the observed effects of harvest. Experimental approaches are necessary as well as comparative studies to assess the effects of spatio-temporal and management variation. Experimentation should be carried out at different ecological levels including, in particular, physiological responses to harvest. In the case of overharvested species, similar unharvested species may sometimes provide adequate proxies for experimentation.

This review illustrates that we have obtained some knowledge of the kinds of management practices that may mitigate or exacerbate the negative impacts of harvest. Further advances will require the co-operation of scientists, managers and local harvesters to document better and assess quantitatively current management practices, as well as to promote and experiment with new ones. A shift in research focus towards assessing successful systems of NTFP extraction may also help us gain a better understanding of the factors that lead to sustainability.

Finally, the data reviewed illustrate that our ability to address effectively all three of the questions above will require re-evaluation and adaptation of the models and methods currently used. Clearly, we need to validate the matrix models used by a large proportion of the studies reviewed, and to determine for what types of species they may or may not provide adequate assessments. There is a need for more studies to account for spatial and temporal variation in environmental and harvest conditions, and to develop or modify models that consider heterogeneity of the landscapes in which NTFP grow, as well as interactions among NTFP populations. Thus, for example, metapopulation, megamatrix and spatially explicit models might provide more realistic assessments of NTFP harvest and also serve to generate hypotheses that can be tested empirically.

This review has focused exclusively on the ecological implications of harvesting. Clearly however, the ecology of any resource used by humans cannot be considered in isolation from political, socio-economic and cultural factors, and indeed is intricately linked to them (Berkes & Folke 2001). The development of sustainable resource-use systems for NTFP will necessitate the concerted efforts of professionals involved in these different fields to work together, and especially in collaboration with NTFP harvesters.

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