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REVIEW ARTICLE

Agroecosystems and Primate Conservation in The Tropics: A Review

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Agroecosystems cover more than one quarter of the global land area (ca. 50 million km^2) as highly simplified (e.g. pasturelands) or more complex systems (e.g. polycultures and agroforestry systems) with the capacity to support higher biodiversity. Increasingly more information has been published about primates in agroecosystems but a general synthesis of the diversity of agroecosystems that primates use or which primate taxa are able to persist in these anthropogenic components of the landscapes is still lacking. Because of the continued extensive transformation of primate habitat into human-modified landscapes, it is important to explore the extent to which agroecosystems are used by primates. In this article, we reviewed published information on the use of agroecosystems by primates in habitat countries and also discuss the potential costs and benefits to human and nonhuman primates of primate use of agroecosystems. The review showed that 57 primate taxa from four regions: Mesoamerica, South America, Sub-Saharan Africa (including Madagascar), and South East Asia, used 38 types of agroecosystems as temporary or permanent habitats. Fifty-one percent of the taxa recorded in agroecosystems were classified as least concern in the IUCN Red List, but the rest were classified as endangered (20%), vulnerable (18%), near threatened (9%), or critically endangered (2%). The large proportion of threatened primates in agroecosystems suggests that agroecosystems may play an important role in landscape approaches to primate conservation. We conclude by discussing the value of agroecosystems for primate conservation at a broad scale and highlight priorities for future research. Am. J. Primatol. 74:696–711, 2012.

Key words: agriculture; agricultural matrix; human-primate conflict; neotropics; paleotropics; primate persistence

INTRODUCTION

The world's human population is expected to increase from 7 billion in 2011 to 9 billion in 2050. As of 2005, there were ca. 2 billion humans in primate range countries. Human populations in these regions are projected to have steep growth through the next three decades [UNFPA, 2007]. The estimated average growth rate from 1980 to 2005 for the Neotropics, Africa, and Southeast Asia was ca. 3% per year, greatly exceeding the world average (1.8% per year) and that of European countries (0.2% per year). Population density in 2005 was estimated at 51 people/km^2 in the Neotropics, 99 people/km^2 in Sub-Saharan Africa and 116 people/km^2 in Southeast Asia [UNFPA, 2007]. The rapidly growing human population and increases in local and global market demands exert an extreme burden on the natural resource base for food production, water, and living space [Lambin & Meyfroidt, 2011] that in turn have significant consequences for native primates. For example, average annual deforestation rates for the period 1990–2005 for the Neotropics have been estimated at 10.9% (15 countries), for Sub-Saharan Africa at 11.3% (30 countries), and for Southeast Asia at 8.9% (13 countries) [FAO, 2007].

Conversion to agriculture has been a major cause of tropical habitat degradation, loss, and fragmentation, and of changes in the distribution of primates [Donald, 2004; Laurance et al., 2002], with

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stochastic forces playing an important role in the decline of populations and the localextinction of species [Chapman et al., 2006; Helne et al., 2004; Mittermeier et al., 2009]. Studies of the consequences of habitat fragmentation on animal communities in the tropics have centered on profiling the biological richness of forest, woodland, and rangeland fragments, and on understanding how species richness is affected by isolation, degradation, edge effects, invasive species, and management practices [Chapman et al., 2006; Laurance et al., 2002]. In this perspective, the focus of landscape studies in the tropics has been the "habitat" and not the "matrix" (i.e. the areas surrounding the native habitat patches of interest). Recently though, some attention has been directed toward the value of the matrix for preserving large segments of biodiversity [Murphy & Lovett-Doust, 2004; Ricketts, 2001].

With interest in protecting their biodiversity, primate range countries have taken important steps to preserve their natural resources by setting up systems of protected areas. According to the World Data Base on Protected Areas of the United Nations (defined by IUCN as "A clearly defined geographical space, recognized, dedicated, and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values."; Dudley, 2008), in 2009, 21% of the land in the Neotropics was protected, 13% in Sub-Saharan Africa, and 11% in Southeast Asia. Although the percentage of protected area has steadily increased in primate range countries, many protected areas are isolated and are relatively small and/or poorly managed to meet long-term conservation goals [Chape et al., 2005; Defries et al., 2005]. Additionally, many important primate populations occur outside of protected areas [Estrada, 2009] and loss or degradation of natural habitats surrounding protected areas is often high, resulting in virtual habitat islands [Bryant et al., 1997; Butynski, 2002; Butynski & Kalina, 1998; Rodrigues et al., 2004; Southworth et al., 2010].

Agroecosystems and Landscape Opportunities for Primates

"Agroecosystems" are ecosystems in which indigenous plants and animals are partially or completely replaced with crops and livestock [Altieri, 2003]. Agroecosystems cover more than one quarter of the global land area (ca. 50 million km^2 in 2000) [Altieri, 2003; Vandermeer, 2003]. Some agroecosystems are highly simplified (e.g. pasturelands, intensive cereal cropping, and monocultures) while others are more complex (e.g. polycultures and agroforestry systems) and support higher biodiversity [Moguel & Toledo, 1999]. Farmers benefit from agroecosystems and natural vegetation by harvesting plants for food, medicine and fuel, hunting wild animals, retention of soil and soil fertility, and water conservation [Altieri, 2003; Vandermeer, 2003]. Ecological services may be further enhanced in heterogeneous landscapes by patches of native habitat and diverse assemblages of agroecosystems providing cash income to rural households and comprise the basis of regional and national economies [Fox et al., 2000; Lenne & Wood, 1999].

More is becoming known about which primate taxa are able to persist well in agroecosystems through various regional case studies. Because of the continuous and extensive transformation of primate habitats to agriculture, and because natural protected areas may not be extensive and diverse enough to preserve primate diversity globally, it is important to explore and synthesize the extent to which agroecosystems are used by primates and to assess the types of benefits and costs of such use. In this review, we examine published information on the use of agroecosystems by primates in habitat countries. The review also includes a general assessment of the potential costs and benefits to human and nonhuman primates of primate use of agroecosystems. We conclude the review by discussing the value of agroecosystems for primate conservation at a broad scale and highlight priorities for future research.

METHODS

We reviewed journal articles, book chapters, several online sources, and the authors' unpublished findings documenting, directly or indirectly, the presence of primates in agroecosystems. Use of agroecosystems here refers to (i) either temporary or permanent residency or use as passageways to reach native habitat and/or other agroecosystems and/or (ii) use of agroecosystems as sources of food (including potential consumption of commercial crops). We grouped the reviewed literature by four major geographic regions: Mesoamerica, South America, Southeast Asia and India, and Sub-Saharan Africa. We summarized the information available on primate presence in agroecosystems by these geographic regions in the first section of our review and in Table I. This section not only describes primates that use agroecosystems in different regions of the world but also highlights the benefits they derive by using them. Further in our review, we also assess the costs to primates of using agroecosystems. Taxonomy follows All the World's Primates (Rowe & Myers, 2012). The conservation status for the taxa detected in agroecosystems was assigned according to the IUCN Red List database (http://www.iucnredlist.org/; last accessed 12 January 2012).

RESULTS

From the information reviewed, we determined that 57 primate taxa were present in 38 types of agroecosystems. Table I provides an overview of the types of agroecosystems used by primates and the primate taxa using them.

Mesoamerica

Primate surveys in fragmented landscapes in Mesoamerica (Southeast Mexico, Guatemala, Nicaragua, and Costa Rica) revealed that mantled howling monkey (*Alouatta palliata*), Yucatán black howler monkey (*A. pigra*), Mexican spider monkey (*Ateles geoffroyi*), white faced capuchin (*Cebus capucinus*), and black-crowned Central American squirrel monkey (*Saimiri oerstedii*) make permanent or temporary use of several arboreal and nonarboreal agroecosystem habitats [Bhagwat et al., 2008; Estrada et al., 2006]. Among the arboreal habitats, shaded coffee (*Coffea* spp.), cacao (*Theobroma cacao*), and cardamom (*Elettaria cardamomum*) plantations stand out for frequency and length of use [Estrada et al., 2006]. Other important agroecosystems were mango (*Mangifera indica*), citrus (*Citrus* spp.), and allspice (*Pimienta dioica*), and mixed plantations such as cacao and coffee or mango, citrus and bananas (*Musa* spp.). Less commonly used as temporary habitats were banana plantations (Estrada et al., 2006). Eucalyptus (*Eucalyptus* spp.) plantations have also been reported to support populations of *A. pigra* in southern Mexico that feed on the native vegetation growing under the eucalyptus, vines growing on the plantation trees, and second growth vegetation in adjacent areas rather than the eucalyptus itself (Bonilla-Sanchez et al., 2012). At the Curú Wildlife refuge in Costa Rica, white-faced capuchins relied on raided coconut (*Cocos nucifera*) and oil palm (*Elaeis guineensis*) crops and provisioned or stolen human foods for over one-half of their total diet (McKinney, 2010; 2011).

The primate species mentioned in the paragraph above have been observed moving between forest patches using intervening arboreal agroecosystems such as shaded coffee and cacao and live fences (single rows of trees planted by humans to parcel their land). Mature live fence trees (≥25 cm DBH) with wide, intact canopies are used by the heavier primates such as *Alouatta* and *Ateles*, while younger live fences support smaller *Cebus* and *Saimiri* monkeys. Using the fences allows primates to avoid movement across open ground (Estrada et al., 2006). Live fences also likely act as a nutritional source to primates. In many cases, monkeys have been observed consuming the leaves and/or fruits of the gumbo-limbo (*Bursera simaruba*), fig (*Ficus* spp.), gliricidia (*Gliricidia sepium*), jobo (*Spondias* spp.), and Geiger (*Cordia* spp.) trees, some of the most common tree species used by local people to build live fences [Harvey et al., 2004]. Permanent and semipermanent residency in agroecosystems may help primate populations persist in fragmented landscapes. In some cases, primates such as howler monkeys (*A. palliata* and *A. pigra)* and spider monkeys (*Ateles geoffroyi*) can persist several decades in shaded coffee and cacao plantations by exploiting the leaves, fruit, and flowers of individuals of major tree species in the Moraceae, Fabaceae, Legumonisae, and Mimosae families, among others, providing shade to cultivated crops [Muñoz et al., 2006]. While *Ateles* is present in these agroecosystems, they used them more often than *Alouatta* as stepping stones to move to adjacent or nearby forest habitats. It is likely that the patchy distribution of the nutritional resources of spider monkeys (e.g. mature fruit) exert important constraints to the length of time they can reside in shaded agroecosystems [Di Fiori & Campbell, 2007]. The importance of agroforests for some primates is further underlined by observations of *A. palliata* and *C. capucinus* moving on the ground to cross open areas to reach cacao and coffee agroforests [Estrada & Coates-Estrada, 1996; Fragazy et al., 2004].

South America

In Guaviare, Colombia, Humboldt's woolly monkey (*Lagothrix lagotricha*) use cacao plantations adjacent to forest fragments. The monkeys feed on the cacao fruit and also use the cacao plantation as a site for resting and feed on tree species providing shade for the cacao trees (Zárate, 2009). The white-fronted capuchin (*Cebus albifrons*) and the Colombian red howler monkey (*Alouatta seniculus*) use the same cacao habitat. While *C. albifrons* feed on the fruits, *A. seniculus* seem to use the agroecosystem as an extension of the forest to rest and feed on the leaves and fruits of trees that provide shade for the cultivar. The same cacao plantations are also visited by the South American squirrel monkey (*Saimiri sciureus)* to feed on ants (Zárate, 2009). In Tinigua National Park, Colombia, *L. lagothricha* have been observed using old cacao plantations to reach the forest and in the experimental farm "Trueno," also Colombia, *L. lagotricha* were observed frequently visiting cacao plantations (P. Stevenson, personal communication).

In four localities in the Peruvian Amazon (Putumayo, Tigre, Marañón, Ucayali) with intense agricultural activity, Bolivian/Peruvian squirrel monkey (*Saimiri boliviensis*) and Ecuadorian squirrel monkey (*S. sciureus macrodon*) occupy remnant forests and make use of adjacent mixed agroecosystems (corn, bananas, and fruit trees) to supplement their food needs [Encarnacion, 1990]. In northern Argentina (Misiones) coexisting southern brown howling monkey (*A. guariba clamitans*) and black-and-gold howler monkey (*Alouatta caraya*) extensively use monocultures of slash pine (*Pinus elliotii*), eucalyptus (*Eucalyptus* sp.), and Brazilian pine (*Araucaraia augustifolia*) bordering native forest. Both *Alouatta*

TABLE I. Agroecosystems Used by Primates for Temporary or Permanent Residency, As Passage-Ways to Reach Native Habitat and/or Other Agroecosystems.

Region/Taxa	Common name	IUCN Red List status	Agroecosystem
Neotropics			
A. palliata	Mantled howler monkey	Least concern	1–5, 12–14, 16–19, 30
A. caraya	Black-and-gold howler monkey	Least concern	7, 8, 9
A. guariba	Southern brown howling monkey	Least concern	7,8,9
A. pigra	Yucatán black howler monkey	Endangered	1, 2, 3, 8, 10, 12, 19, 30
A. seniculus	Colombian red howler monkey	Least concern	2
A. geoffroyi	Geoffroy's spider monkey	Endangered	1, 2, 3, 10, 17, 19
C. nigrifrons	Black-fronted titi monkey	Near threatened	8
C. kuhlii	Wied's Black-tufted-ear marmoset	Near threatened	2
C. albifrons	White-fronted capuchin	Least concern	2
C. capucinus	White-throated capuchin	Least concern	10, 15, 19, 36
S. nigritus	Black-horned capuchin	Near threatened	7, 8
L. lagotricha	Humboldt's woolly monkey	Vulnerable	2
L. chrysomelas	Golden-headed lion tamarin	Endangered	2
S. boliviensis	Bolivian/Peruvian squirrel monkey	Least concern	6
S. oerstedii	Black-crowned Central American squirrel monkey	Vulnerable	15, 17, 19, 30
S. sciureus macrodon	South American squirrel monkey	Least concern	34
Southeast Asia			
H. agilis	Agile gibbon	Endangered	20, 21, 22
H. lar	Lar gibbon	Endangered	33
S. syndactilus	Siamang	Endangered	20, 21, 22
M. fascicularis	Crab-eating macaque	Least concern	2, 24
M. mulatta	Rhesus monkey	Least concern	20
M. nemestrina	Southern pig-tailed macaque	Vulnerable	33
M. radiata	Bonnet macaque	Least concern	1
M. tonkeana	Tonkean macaque	Vulnerable	23, 25
M. ochreata brunescens	Muna-buton macaque	Vulnerable	37
P. abelii	Sumatran orangutan	Critically endangered	33
P. thomasi	Thomas's langur	Vulnerable	33
P. rubicunda	Maroon leaf monkey	Least concern	20, 21, 22
S. entellus	Northern Plains gray langur	Least concern	1
T. geei	Gee's golden langur	Endangered	20
T. villosus	Griffith's silver langur	NA	33
T. dentatus	Dian's tarsier	Vulnerable	4, 11
Sub-Saharan Africa			
C. lhoesti	L'Hoest's monkey	Vulnerable	26
C. ascanius	Red-tailed monkey	Least concern	13, 15, 17, 26, 27
C. erythrotis	Red-eared monkey	Vulnerable	1, 2, 13
C. mitis	Blue monkey	Least concern	13, 15, 17, 26, 27
C. pygerythrus	Vervet	Least concern	15, 17, 27, 29
C. guereza	Guereza	Least concern	26
E. patas	Patas monkey	Least concern	29
G. senegalensis	Northern lesser galago	Least concern	28
G. beringei	Eastern gorilla	Endangered	13
L. ugandae	Uganda grey-cheeked mangabey	Least concern	26
M. leucophaeus	Drill	Endangered	13
P. troglodytes	Common chimpanzee	Endangered	13, 15, 17, 26, 27, 38
P. anubis	Olive baboon	Least concern	13, 15, 17, 26, 27, 29
P. cynocephalus	Yellow baboon	Least concern	13, 15, 17, 27
P. rufomitratus	Tana River red colobus	Least concern	26

TABLE I. *Continued.*

Region/Taxa	Common name	IUCN Red List status	Agroecosystem
Madagascar			
A. laniger	Gmelin's woolly lemur	Least concern	8
C. major	Geoffroy's dwarf lemur	Least concern	8
E. macaco macaco	Black lemur	Vulnerable	32
H. griseus	Eastern lesser bamboo lemur	Vulnerable	8
L. catta	Ring-tailed lemur	Near threatened	35
E. fulvus	Common brown lemur	Near threatened	8, 31
L. mustelinus	Weasel sportive lemur	NA	8, 32
M. rufus	Rufous mouse lemur	Least concern	8
I. indri	Indri	Endangered	8
P. verreauxi	Verreaux's sifaka	Vulnerable	31

In many cases, these habitats supply or supplement primates' feeding demands. Not listed are cash-crops raided by some primates. Taxonomy follows (Rowe & Myers, 2012) and IUCN Red List (last accessed, January 2012). The IUCN Red List status for each taxa was determined from http://www.iucnredlist.org (last accessed 12 January 2012). The key to Agroecosystem Numeric Codes is below; references for the listed primates can be found within the corresponding sections of this paper.

1, Shaded coffee (*Coffea* spp.); 2, Shaded cacao (*Theobroma cacao*); 3, Shaded coffee and cacao; 4, Shaded cacao and gliricidia (*Gliricidia sepium*); 5, Mixed: cacao, coconut (*Cocos nucifera*) and banana (*Musa* spp.); 6, Mixed: banana (*Musa* spp.), abiu (*Inga edulis*), shimbillo (*Inga* spp.), Amazon tree grape (*Pourouma cecropiaefolia*; 7, Slash pine (*Pinus elliotii*); 8, Eucalyptus ((*Ecucalyptus* spp.); 9, Brazilian pine (*Araucaraia augustifolia*); 10, Mixed: cacao, coffee, citrus, banana; 11, Mixed: cacao, gliricidia, bamboo (Poaceae), alang-alang grass (*Imperata cylindrical*); 12, Shaded cardamom (*Elettaria cardamomum*); 13, Banana; 14, Citrus (*Citrus* spp.); 15, Oil palm (*Elaeis* spp.); 16, Allspice (*Pimienta dioica*); 17, Mango (*Mangifera indica*); 18, Mango, citrus, banana; 19, Live fences (*Bursera simaruba, Gliricidia sepíum*); 20, Rubber (*Hevea brasiliensis*); 21, Damar (*Shorea javanica*); 22, Durian (Durio zibethinus); 23, Papaya (*Carica papaya*); 24, Mixed: Forest-rice (*Oryza* spp.), bamboo (Poeceae)-rice and dry forest-tamarind (*Tamarindus indica*); 25, Sugar palm (*Arenga pinnata*); 26, Pine (*Pinus* spp.); 27, guava (*Psidium guajava*); 28, Firestick (*Euphorbia tirucalli*); 29, Prickly pear (*Opuntia* spp.); 30, Forestry plantation; 31, Mixed tree plantations: mango and *Stereospermum arcuatum*; 32, Mixed plantation: mango, coffee, coconut, papaya; 33, Mixed: oil palm, rubber, forest remnants; 34 Mixed: corn, bananas, fruit trees; 35, mixed fruit tree plantations; 36, coconut plantation; 37 mixed crops of sweet potato and fruit trees; 38, mosaic of thicket, cultivated fields, and orchards.

NA = not available.

species feed on pine cones and use the trees as sleeping sites [Agostini et al., 2010a, b]. In Brazil's southern Atlantic forests, *A. caraya* lives in eucalyptus plantations [Mattjie-Prates, 2007] and black-fronted titi monkeys (*Callicebus nigrifrons*) also are reported in eucalyptus in Canareira State Park (São Paulo, Brazil). In both cases, the primates use eucalyptus trees as sources of food [Trevelin et al., 2007].

Shaded-cacao agroforest, known in Brazil as cabruca, is the predominant habitat type throughout the eastern portion of the golden-headed lion tamarin (*Leontopithecus chrysomelas*) distribution [Raboy et al., 2010]. *L. chrysomelas* is endangered and endemic to Brazilian Atlantic Forest [IUCN, 2011]. Cabruca harbors important and sometimes abundant dietary resources for *L. chrysomelas* [Alves, 1990; Oliveira et al., 2010, 2011; Raboy et al., 2004], including various species of fruit and animal prey. Some *L. chrysomelas* groups have now been documented living exclusively in cabruca [Oliveira et al., 2011]. These groups had similar group size and composition to groups in other types of forest, although home range sizes were significantly smaller. The density, number of litters per year and weight of individuals were higher for cabruca-dwelling *L. chrysomelas* compared to primary forest groups. The abundance of jackfruit (*Artocarpus heterophyllus*; up to 55% of the total fruit consumed) and insects living within bromeliads in cabruca may explain these results (L. Oliveira, unpublished data). Although jackfruit was a critical species for the *L. chrysomelas* groups studied—both abundant (temporally and spatially) and predictable [Oliveira et al., 2011], it may not be present in all cabruca. It remains unknown how lion tamarins might thrive in cabruca areas without jackfruit.

Despite the potential drawbacks of living in a human-modified habitat that include exposure to predators, modified or limited substrates for movement, increased hunting, and disease transmission, the importance of cabruca habitat to *L. chrysomelas* is apparent. A synthesis of information from the aforementioned behavioral and ecological studies on GHLTs in cabruca (Oliveira et al., 2010, 2011; Raboy et al., 2004) and landscape modeling (Raboy et al., 2010; Zeigler et al., 2010) suggests that not only do GHLTs make good use of cabrucas, but also populations may actually be less vulnerable to negative genetic and demographic effects of habitat fragmentation in areas where cabruca connects native forests as opposed to areas that lack such connectivity. Demographic simulation modeling of populations living in differing regions in the *L. chrysomelas* landscape indicated that local population declines were more likely to occur in severely fragmented forests surrounded by pasture matrix than in forest fragments linked by cabruca (Raboy et al., 2010; Zeigler et al., 2010). Raboy et al., [2010] also indicated that as the westerly edge of the range recedes to the east due to severe fragmentation and resulting local extinctions, cabruca will harbor a larger proportion of the remaining *L. chrysomelas* population than before. Changes in the management of this agroforest, such as increasing the density of shade trees, replacing dead trees with species that are most used by *L. chrysomelas*, improved market price for cocoa or farmer incentives [Oliveira et al., 2010, 2011] are vital to *L. chrysomelas* conservation.

South East Asia and India

In Gulung Palung National Park, Kalimantan, maroon leaf monkeys (*Presbytis rubicunda*) and agile gibbons (*Hylobates agilis*) are found in agroforests [Salafsky, 1993]. *P. rubicunda*, rhesus monkeys *(Macaca mulatta)*, and siamangs (*Symphalangus syndactilus*) are present in rubber (*Hevea brasiliensis*) and dammar (*Shorea javanica*) agroforests, and also in durian (*Durio zibethinus*) agroforests in Sumatra where they occur in similar densities as they do in primary forests [Michon & de Foresta, 1995].

Dian's tarsiers (*Tarsius dentatus*) in Sulawesi, Indonesia, occupy mixed-species plantations of cacao and gliricidia (*Gliricidia sepium*) with interspersed patches of dense shrub, bamboo (*Bambusa* spp.), alang-alang (*Imperata cylindrical*), and corn outside native forests [Merker et al., 2005]. It appears that limited human disturbance does not pose a major threat to *T. dentatus*. The availability of sleeping sites, such as fig trees (*Ficus* spp.), bamboo (*Bambusa* spp.), and dense shrubs, was not limited in cacao plantations and there was no evidence of predation. The density of *T. dentatus* in plantations was, however, significantly lower (45 individuals/km^2) than in undisturbed forest (268 individuals/km^2) [Merker et al., 2005]. *T. dentatus* are able to adapt to small-scale agroforestry (coffee or cacao) in combination with selective logging of adjacent forest [Merker & Mühlenberg, 2000] because disturbance opens the forest canopy and increases forest heterogeneity that subsequently supports higher arthropod diversity and abundance [Merker et al., 2005]. Merker [2006] asserts that the small ranges and travel distances in areas with small-scale agroforestry indicate that even disturbed habitats still provide good conditions for tarsiers.

In Batang Serangan northern Sumatra, a small population of the Sumatran orangutan (*Pongo abelii*) has been reported living for several decades in a mixed agroforest system composed of oil palm (*Elaeis guineensis*), rubber trees (*Hevea brasiliensis*), and remnant forest, and feed on jackfruit and durian, among others [Campbell-Smith et al., 2010]. In addition to orangutans, other primates living in this agroecosystem are Thomas's langur (*Presbytis thomasi*), common long-tailed macaque (*Macaca fascicularis fascicularis*), southern pig-tailed macaque (*Macaca nemestrina*), Lar gibbon (*Hylobates lar*), and Griffith's silver langur (*Trachypithecus villosus*) [Campbell-Smith et al., 2010].

Riley [2008] studied the ranging patterns and habitat use of Sulawesi Tonkean macaques (*Macaca tonkeana*) in human-modified habitats, some of which included agroforestry/agricultural areas within forests. *M. tonkeana* were tolerated by humans due to the indigenous Lindu human–macaque folklore [Riley, 2007a, 2010]. One study group spent less time in continuous forest and more time in agroforestry areas than expected. Although 66% of the group's home range consisted of cacao and coffee agroforest, neither crop was exploited by this group. The group frequently consumed papaya (*Carica papaya*) from the one mixed-fruit tree garden within its range [Riley, 2007b]. Primate surveys across Bali, Indonesia, revealed that six of 29 sites which support *M. fascicularis* comprise a mix of forest rice (*Oryza sativa*), bamboo rice, and dry forest-tamarind (*Tamarindus indica*) [Riley & Fuentes, 2011]. The Muna-buton macaque (*Macaca ochreata brunnescens*) in Buton island in southeast Sulawesi, Indonesia, uses mixed plantations of sweet potato (*Ipomoea batatas*) and fruiting trees, eating both the planted fruit and potatoes (Priston et al., 2012).

A relict population of Gee's golden langurs (*Trachypithecus geei*) has lived for several decades in a rubber plantation in Kokrajhar District, Assam, India, where they coexist with *M. mulatta* [Mehdi et al., 2004]. Bonnet macaques (*Macaca radiata*) and Northern Plains gray langur (*Semnopithecus entellus*) use coffee plantations bordering a protected area in Western Ghatts, India [Bali et al., 2007]. Such coffee plantations serve as buffers for forest reserves and improve connectivity between them. However, the increasing conversion of native forest to silver oak (*Grevillea robusta*), combined with hunting, threatens the quality of this matrix habitat for these primates [Bali et al., 2007].

Sub-Saharan Africa

In Sub-Saharan Africa, the use of agroecosystems by primates is common, widespread, and important to their conservation. On Bioko Island, Equatorial Guinea, two threatened species, red-eared guenon (*Cercopithecus erythrotis*) and drill (*Mandrillus leucophaeus*), forage in banana (*Musa* spp.) plantations, and *C. erythrotis* also forages in shaded cacao and coffee plantations (T. Butynski, personal communication). In Kibale National Park, south-west Uganda, many primate taxa, including eastern red colobus (*Procolobus rufomitratus*), guereza (*Colobus guereza*), Uganda grey-cheeked mangabey (*Lophocebus ugandae*), olive baboon (*Papio anubis*), blue monkey (*Cercopithecus mitis*), red-tailed monkey (*Cercopithecus ascanius*), L'Hoest's monkey (*Cercopithecus lhoesti*), and common chimpanzee (*Pan troglodytes*), forage in pine (*Pinus* sp.) plantations next to indigenous submontane forest (T. Butynski, personal communication). In the same park, *C. guereza* regularly visit eucalyptus plantations to feed on the trees (Harris & Chapman, 2007). In Bwindi Impenetrable National Park, south-west Uganda, the Eastern gorilla (*Gorilla beringei*) and *P. troglodytes*, both endangered species, forage in banana plantations (T. Butynski, personal communication).

In Kenya and Tanzania, guava (*Psidium guajava*), mango (*Mangifera indica*), oil palm (*Elaeis* sp.), and banana plantations, either cultivated or abandoned, are often used by Sykes's monkey (*Cercopithecus mitis*), *C. ascanius*, vervet (*Chlorocebus pygerythrus*), *P. anubis*, yellow baboons (*Papio cynocephalus*), and *P. troglodytes* (Y. de Jong and T. Butynski, personal communication). In Kenya, the Northern lesser galago (*Galago senegalensis*) occupies firestick (*Euphorbia tirucalli*) fence rows placed to protect and demarcate gardens and small-scale farms (T. Butynski and Y. de Jong, personal communication). Even barbed wire and electric wire fences provide some benefit to primates. For example, in Kenya, the patas monkey (*Erythrocebus patas*) uses fence posts as sites from which to scan for predators and rivals and along which to move through open areas [Chism & Rowell, 1988]. In Bossou, Republic of Guinea, West Africa, chimpanzees regularly use a mosaic of thicket, cultivated fields, and orchards bordering the forest. Here, they harvest food from about 17 cultivated plants, and because the Manon ethnic group holds the chimpanzees as a sacred totem, crop damage is somewhat tolerated. The study points out that these anthropogenic habitats seem to provide important amounts of food to chimpanzees in times of fruit scarcity (Hockings et al., 2012).

In eastern Madagascar, seven sympatric species of Strepsirhini (Gmelin's woolly lemur, *Avahi laniger*; Geoffroyi's dwarf lemur, *Cheirogaleus major*; Eastern lesser bamboo lemur, *Hapalemur griseus*; Indri, *Indri indri*; common brown lemur, *Eulemur fulvus*; weasel sportive lemur, *Lepilemur mustelinus*; ruffous mouse lemur *Microcebus rufus*) are reported living in eucalyptus plantations. Some of these Strepsirhini used the plantations mainly for resting and to travel from one patch of native forest to another, but they also feed on leaves, fruits, and flowers of plants of all layers, including flowers of *Eucalyptus sp*. [Ganzhorn, 1987]. The same study reports groups of Verreaux's sifaka (*Propithecus verreauxi*) as permanent residents of mixed mango (*Mangifera indica*) and vavaloza trees (*Stereospermum arcuatum*) where they also feed on fruit and leaves of mangos and on the flowers and leaves of *S. arcuatum*. Other primates seen in these mixed plantations were *A. laniger*, *L. mustelinus*, and *E. fulvus*. [Ganzhorn, 1987; Ganzhorn & Abrahams, 1991]. Black lemurs (*Eulemur macaco macaco*) were reported living in mixed plantations of mango, coffee, coconut, and papaya in northwestern Madagascar where they feed on mangos, papayas, palm fruits, and flowers of the Dypsis palm (*Dypsis* spp.), and crossberry fruits (*Grewia* spp.) [Simmen et al., 2007]. Ringtailed lemurs (*Lemur catta*) will go into mixed fruit tree plantations to eat ripe fruit [R. Sussman, personal communication].

The Costs to Primates of Using Agroecosystems

Hunting

Hunting is a major threat to primate populations in West and Central Africa [Hearn et al., 2006; Robinson & Bennett, 2000; Rose et al., 2003], and at some sites in East Africa [De Jong et al., 2008]. Economic and cultural incentives in these regions sustain the bushmeat trade and primate species are consumed domestically or traded in markets. Similar but less intense hunting pressures upon primate populations exist in the Neotropics [Fa et al., 2004; Jerozolimski & Peres, 2003]. Primates living in human-modified landscapes, agroecosystems, and in matrix habitats are at greater risk of being hunted by humans and domestic dogs and by open habitat raptors and other predators. In addition, farmers hunt in and around their fields for home consumption, local or urban sale, or to eradicate what they believe are pests [Bennett et al., 2006]. Even in areas where monkeys such as *M. fascicularis* are considered sacred and where fire arms are not allowed, such as in Bali, Indonesia, people use air guns to shoot macaques (Schillaci et al., 2010). Older primates in agroecosystems may become victims of hunters seeking young individuals for the pet trade. For example, in southeast Mexico, *A. pigra* and *A. palliata* infants are easily captured by killing females in groups that occasionally use citrus and banana groves (Estrada, unpublished data). In general, primates venturing into agricultural fields and using these as stepping stones when moving across the human-modified landscape or as a source of food greater are much more exposed to hunters due to lack of dense vegetation cover.

Presence/absence of substrate in agroecosystems

Not all arboreal agroecosystems are suitable for permanent residency by primates. For example, primates in Mesoamerica such as *Alouatta*, *Ateles*, *Cebus*, and *Saimiri* did not reside permanently in citrus, allspice, and mango groves, and only occasionally visited banana plantations [Harvey et al., 2004]. These plantations usually bordered primate habitat or were connected with corridors. Several factors may discourage residency by primates in these plantations; (i) wide inter-row space between the cultivated plants suggests lack of suitable structure for arboreal locomotion, (ii) extreme climatic conditions such as high exposure to solar radiation, high temperatures, and low humidity in these habitats, and (iii) greater exposure to potential predators, including to humans and dogs. In the case of live fences, their narrow width (generally averaging <8 m) [Chacón & Harvey, 2006] supports their use as passageways but not as true habitats.

Unlike citrus, allspice, and mango groves, *S. oesterdii* and *C. capucinus* can reside in large (>100 ha) African oil palm (*Elaeis guineensis*) plantations because these contained small patches of other trees where the monkeys found shelter. These taxa probably persist in these plantations due to a relatively high abundance of potential food items represented by the sugary pulp encasing the seed of palm fruits and on insects and small vertebrates found in palm fronds and on tree trunks. In shaded agroecosystems, such as cacao, coffee, mixed cacao/coffee, and cardamom, the complexity of the mid and upper canopy, including numerous epiphytes, vines, lianas, and other climbing plants offer many potential food resources, shelter, resting sites, and cover to primates using these habitats [Estrada & Coates-Estrada, 1996; Estrada et al., 2006].

Despite the above advantages, the above features, increased exposure to predators also has been suggested as a cost to *L. chrysomelas* living in cacao plantations in Brazil. The number of encounters per hour of observation between *L. chrysomelas* with potential predators was almost four times higher in cacao plantations compared to other vegetation types [Oliveira & Dietz, 2011]. In their study, Oliveira and Dietz suggest that due to possible lower tree density and the substitution of understory by cacao plants, the canopy has reduced complexity thus exposing the tamarins to raptors such as the mantled hawk (*Leucopternis polionotus*) and the zone-tailed hawk (*Buteo albonotatus*) and to carnivores such as the tayra (*Eira barbara*). Furthermore, lower tree density leads to decreased availability of sleeping sites (tree holes) that forces *L. chrysomelas* to reuse sleeping sites with greater frequency [Oliveira et al., 2010; Raboy et al., 2004] causing an increased threat that predators learn the position of the sleeping site [Fenton et al., 1994]. The absence of supporting substrates, such as lianas that did occur in neighboring mature forest, was also observed in cabruca [Raboy et al., 2004], potentially impeding escape from predators. It is possible that a similar pattern of increased exposure to predators may occur in other types of agroecosystems used by primates as they are, by definition, structurally less complex than a mature forest.

The regional review documented in earlier pages suggest that in Sub-Saharan Africa, Madagascar, and South East Asia, many small (e.g. galago, Geoffroyi's dwarf lemur, Dian's tarsier), medium (e.g. colobus, macaques, gibbons), and large (e.g. chimpanzees and orangutas) size primates benefit from the presence of arboreal plantations such as shaded cacao and coffee, shaded cardamom, mango, rubber, among others, as these provide enough substratum for locomotion and other activities as well as shelter and additional food.

Transmission of parasites and diseases

Primates are particularly vulnerable to the spread of parasitic infections because their sociality and group living facilitates parasite transmission [Chapman et al., 2005]. Habitat fragmentation increases the susceptibility of primates to infection by gastrointestinal parasites. Monkeys in small fragmented habitats may have to come to the ground to move from one patch to another and/or may drink ground water with the possibility of acquiring parasites, and because of proximity to human settlements and to domestic animals, may also be exposed to parasitic vectors or intermediate hosts. In some cases, this may result in high mortality and morbidity [Shalk & Forbes, 1997]. The close proximity of human to nonhuman primates in agroecosystems may increase the risk of disease and parasite transmission among humans, nonhuman primates, and other animals [Altizer et al., 2003; Chapman et al., 2005; Gillespie et al., 2005a,b]. In Kibale National Park, two parasite genera, *Ascaris* and *Giardia* have high prevalence in the human populations occur in *P. rufomitratus* in forest fragments, but *P. rufomitratus* in continuous forest displayed a lower prevalence for these parasites [Gillespie et al., 2005b]. In Tanzania, a population of *P. anubis* living in close proximity with people was infected with yaws (*Treponema pertenue*), typically transmitted through flies. The close proximity of humans, *P. anubis*, and flies likely provided optimal conditions for transmission of this disease [Wallis & Lee, 1999]. In another region of Africa, *G. beringei* and *P. troglodytes* living in fragmented habitats and exploiting agroecosystems are contracting diseases and parasites from humans and their livestock [Butynski, 2001; Palacios et al., 2011; Woodford et al., 2002]. At a cacao plantation in southeast Mexico *A. palliata* had a high prevalence of coccidia (*Eimeria* spp.), commonly found in poultry and cattle [Trejo and Estrada, unpublished data].

In general, Old World monkeys and apes seem to be more susceptible to human-borne diseases, such as Tuberculosis, Shigellosis, Salmonellosis, Colibacillosis, Klebsiella pneumoniae, Hemophilus influenzae, Malaria, and Amoebiosis, among others (T. R. Schoeb, http://netvet.wustl.edu/species/primates/primate2.txt; accessed March 2012) than New World primates and Strepsirhines. Old World monkeys and apes may thus be at a great risk of acquiring human-borne parasites and diseases when in agroecosystems. A particular case of pathogens introduced or exacerbated by human activity has been Ebola virus outbreaks in gorillas and chimpanzees, resulting in population declines [Bermejo et al., 2006]. Such events are probably the result of increased human activities that cause pathogen introductions or shifts in host (Nunn et al., 2003). A study in Uganda showed that diversity of bacteria harbored by humans and livestock (e.g. *Escherichia coli*) was similar to those of red-tailed guenons, which habitually enter human settlements to raid crops, than to bacteria of other primate species, suggesting that anthropogenic disturbance seems to influence interspecific bacterial transmission (Goldberg et al., 2008).

The Costs to Humans of Primates Using Agroecosystems

Crop-raiding

Cropland agroecosystems in the tropics often border primate habitat. Consequently, crop-raiding is a major cause of conflict with humans [Goldsmith 2005; Hockings & Humle, 2009; Rijksen, 2001; Salafsky, 1993]. As a result, some primates are viewed as a serious menace to agriculture in many tropical countries leading in some cases to the implementation of primate control or eradication plans [Hockings & Humle, 2009; Lackman-Ancrenaz et al., 2001; Marchal, 2005; Rijksen, 2001]. Furthermore, crop damage may lead to the clearance of natural vegetation to eliminate or discourage crop-raiding [De Jong, 2004; Osborn & Hill, 2005].

In Mesoamerica primates, such as *A. palliata*, *A. pigra*, *A. geoffroyi*, *Cebus capucinus*, and *S. oerstedii*, cause limited damage to cacao, coffee and cardamom, banana, mango, citrus, and allspice, but the loss causes no significant impact upon the cash crops and thus farmers tolerate the presence of primates in the agroecosystems [Estrada et al., 2006; McKinney, 2010; Muñoz et al., 2006; Rosales-Meda et al., 2007]. In Peruvian Amazon (*Saimiri boliviensis peruviensis*) and Ecuadorian squirrel monkey (*S. sciureus macrodon*) raid mixed agroecosystems of corn, bananas, and fruit trees when food is scarce in the forest remnants they occupy [Encarnacion, 1990]. In northern Argentina, black capuchins (*Sapajus nigritus*) have been observed visiting slash pine plantations where they attack young pines (4–8 years of age) peeling the bark, with many trees dying (I. Agostini, personal communication). In general crop-raiding is not as widespread as in the Paleotropics [Gonzales-Kirchner & Sainz de la Maza, 1998].

In southeast Sulawesi, Indonesia, Buton island macaque (*Macaca ochreata brunnescens*) consistently raid farms where sweet potato (*Ipomoea batatas*), maize (*Zea mays*), and cassava (*Manihot esculenta*) are cultivated, along with a variety of fruits such as jackfruit (*A. heterophyllus*) and papaya (*Carica papaya*) [Priston et al., 2012]. In Bali, Indonesia, *M. fascicularis* raids crops, but the amount of damage is quite low [Riley & Fuentes, 2011]. Orangutans (*P. abelii*) have been reported to raid fruit crops in Batang Serangan, northern Sumatra, and farmers placed orangutans as the third most frequent and fourth most destructive crop pest, after Thomas' leaf monkey (*P. thomasi*) in two localities [Campbell-Smith et al., 2010].

In Africa and Asia, primates are responsible for 50–70% of the crop damage in agricultural areas surrounding protected areas [Hill, 2005; Naughton-Treves et al., 1998]. Species in the widespread genera *Macaca*, *Papio*, *Chlorocebus*, and *Cercopithecus* are the most frequent primate pests [Paterson & Wallis, 2005; Priston et al., 2012; T. Butynski and Y. de Jong, personal communication]. In Kenya, *P. anubis*, *P. cynocephalus*, *C. mitis*, and *C. pygerythrus* are the main species involved in crop-raiding. During 2005–2009, the Kenya Wildlife Service received notice of nearly 3,000 cases of primate–human conflict. The actual number of cases is probably several times higher as the vast majority is unreported (B. Kavu, personal communication through T. Buynski). Corn and fruits are the crops most frequently raided by primates in Kenya. *Erythrocebus patas* in western Kenya live in an agricultural matrix that includes degraded riverine vegetation. The *E. patas* feed on crops, especially corn, and therefore, are treated as vermin [De Jong, 2004, 2008]. In addition to crop loss, people sometimes fear for their personal safety when near primates [Campbell-Smith et al., 2010; Madden, 2006; McLennan, 2008].

Ethnoprimatology research shows that in some localities farmers cultural and religious beliefs and perceptions contribute to the protection of primates in those regions (Courmier, 2006; Campbell-Smith et al., 2010; Riley, 2010). Because of this belief system, farmers tolerate a certain degree of crop damage by primates depending upon factors such as crop type, invested effort in crop production, and market value of the crop [Hockings & Humle, 2009; Hockings et al., 2009, 2012].

A survey of published reports in PrimateLit, a bibiliographic database for primate literature, (http://primatelit.library.wisc.edu/; accessed August 2010) making reference to crop-raiding by primates resulted in 535 "hits" of which 53% were for Asia, 40% for Africa, and 8% for the Neotropics. When crop-raiding "hits" for each region were expressed as percent of total literature "hits" (regardless of research topic) for each region, crop-raiding "hits" for Asia accounted for 3.0% ($N = 9{,}461$ "hits"), for Africa 1.8% ($N = 11{,}549$), and for the Neotropics 0.5% ($N = 7{,}945$), suggesting that crop-raiding is less common in the Neotropics than in the Paleotropics. The degree of terrestriality Old and New World primates may relate to such differences. Neotropical primate species assemblages are generally arboreal in contrast to the many semiterrestrial forms of the Paleotropics.

The Benefits to Humans of Primates Using Agroecosystems

Primates as seed dispersers

Studies on the ecological value of forest-dwelling primates have stressed their role as potential seed dispersers. Evidence indicates that the role primates play in seed dispersal is essential for the regeneration of plant species and cannot be compensated for by other taxa, stressing the importance of primate persistence for continuing forest dynamics [Bollen et al., 2004; Chapman & Onderdonk, 1998; Clark et al., 2001; Jordano et al., 2011] and for local economies [Kone et al., 2008; Lambert & Garber, 1998]. Although there has been relatively few studies on this topic for primates using agroecosystems, it is likely that primates disperse the seeds of shade trees in a similar manner to the well-documented process in native forest. In so doing, the primates may favor the persistence and regeneration of their own fruit resources or even facilitate the process of regeneration by dispersing seeds to the edge of the plantations. In some cases, this process may be of interest to farmers. For example, in southern Mexico, seedlings from primate-dispersed seeds in some shade-cacao plantations are harvested by humans for reforestation within and outside the plantation (A. Estrada, personal observation). In Southern Bahia, Brazil, *L. chrysomelas* that inhabit shade-cacao agroforest areas carry seeds in and out of habitats. Of the seeds that passed through their digestive tract, 47% were returned to the shade-cacao agroforest, 33% to mature forest and 20% to secondary forest [Cardoso et al., 2008].

Contribution of primates to primary productivity

Primates in agroecosystems may aide in cycles of primary productivity in the habitats in which they are found. Their foraging activities remove foliage and dislodge branches and other organic matter in canopy trees that provide shade to underlying cultivars such as cacao, coffee, and cardamom (*Elettaria* sp.), among others. This stimulates growth of foliage and accelerates the addition of organic matter to the soil [Estrada et al., 2006]. Primate feces may add important nutrients to the soil as well. For example, the feces of *A. palliata* are nutrient-rich [Nagy & Milton, 1979], containing 1.8–2.1% nitrogen (N) and 0.3–0.4% phosphorus (P; based on dry mass) [Milton et al., 1980]. In contrast, leaf litter is approximately 1% N and 0.04% P for tropical moist forests [Feeley, 2005]. In Venezuelan forests, soil N under trees in which *A. seniculus* defecated was 1.6–1.7 times greater than that in control sites (test plots in surrounding soil), and P was 3.8–6.0 times greater under trees used by this primate than in the surrounding soil [Feeley, 2005]. High dispersal of nutrients via howler feces in agroecosystems, such as forest-shaded cacao and coffee, may result from the howlers' daily movements benefiting not only the shade trees that sustain the howlers but also the cultivated plants that grow underneath [Muñoz et al., 2006; Stevenson, 2010]. For example, on-going research in southeast Mexico indicates a gross contribution of 121 kg per year of N and of 22 kg per year of P to the soil of a 10 ha cacao plantation by a group of 22 mantled howler monkeys [Estrada, unpublished data].

Primates and insect populations in agroecosystems

Population outbreaks of some insect species can have a devastating effect on agroecosystems because the insects severely defoliate the trees or attack the fruit or the bark. The foraging activities of insect-eating primates may be important in ameliorating the impact of insect pests. In Guaviare, Colombia-shaded cacao plantations are visited by the common squirrel monkey (*S. sciureus*) to feed on ants [Zárate, 2009]. In Amazonian Peru, *S. boliviensis* and *S. sciureus macrodon* feed on insects in mixed agroecosystems (corn, bananas, and fruit trees) to supplement their dietary needs [Encarnacion, 1990]. Insect foraging is common in *L. chrysomelas* living in cacao plantations in Brazil [Raboy et al., 2004]. Insect-eating has also been reported for *T. dentatus* in mixed-species plantations of cacao and gliricidia in Sulawesi, Indonesia [Merker et al., 2005].

Primates and ecotourism

Occasionally, plantation managers/owners benefit from the presence of primate groups, especially when tourism generates extra income. In southeast Mexico, for example, a cacao plantation successfully integrated the presence of *A. palliata* into a marketing and conservation strategy attracting tourists (see http://www.fincacholula.com.mx). In Bali, Indonesia, Balinese tolerate damage to crops by *M. fascicularis* because of the economic yield from tourism [Riley & Priston, 2010]. However, economic benefits derived from tourism are localized and most areas do not benefit from this due to their remoteness or transitory macaque populations. Recent research indicates that these communities are affected the greatest by crop raiding, resulting in a negative human–macaque interaction (Lane et al., 2010).

DISCUSSION

About 50% of the world's estimated 660 primate taxa are threatened with extinction as a result of human pressures [Mittermeier et al., 2009]. High human population growth translates into local and landscape level agricultural intensification that places enormous pressure on natural habitats in many primate range countries, including protected areas. In addition, most protected areas are surrounded by, or are part of, a matrix of human-altered habitats [Mora & Sale, 2011; UNDP, 2006]. This situation will increase not only the extent of anthropogenic pressures but also the difficulty in successfully enforcing protected areas. Primate source countries continue efforts toward improving and increasing the number and/or size of protected areas, but there is a clear and urgent need for the development of additional solutions for compensating primate habitat loss. One avenue in this direction is to further explore the value of agroecosystems for primate conservation in fragmented landscapes [Schwitzer et al., 2011].

Our review showed that populations of 57 primate taxa use 38 types of agroecosystems, but these numbers are probably an underestimate as there are very few studies focusing on this issue. Agroecosystems used by primates in human-modified landscapes represent additional availability of vegetation, potential food resources, shelter, and the possibility to disperse and find conspecifics. In a fragmented landscape where the matrix is agroforest or other types of arboreal agroecosystems, the presence of networks of linear strips of vegetation represented by live fences, hedge rows, and/or riparian corridors supports dispersal of primates. Importantly, agroecosystems bordering forest fragments or natural protected areas may be an important buffer protecting against edge effects such as desiccation caused by high temperatures and low humidity, soil compactness, wind penetration, and resulting tree mortality [Laurance, 1991]. Conservation approaches using agroecosystems may incorporate wildlife-friendly farming or high-intensity farming with land sparing for nature. For example, a recent study of cacao agroforestry systems around Lore Lindu National Park in Sulawesi, Indonesia, showed that it is possible to combine moderate shade, adequate labor, and input level (pesticides and herbicides) with a complex habitat structure to facilitate biodiversity of butterflies, birds, rodents, spiders, and amphibians as well as high-crop yields [Clough et al., 2011]. The review also showed that 49% of the taxa recorded in agroecosystems are classified as threatened or near threatened in the IUCN Red List database (http://www.iucnredlist.org) (Table I), further stressing the value of agroecosystems for primate conservation in human-modified landscapes in the tropics.

Caveats to Consider

The use of agroecosystems by primate taxa increases the exposure of primates to environmental hazards, human conflict, predation, zoonosis, and hunting pressures. Moreover, forest fragments and agroecosystems may act as ecological sinks and traps for primate populations [Battin, 2004; Murphy & Lovett-Doust, 2004]. For example, at Los Tuxtlas, Mexico *Alouatta palliata* and *Ateles geoffroyi* are absent in 62% and 84%, respectively of the surveyed plantations ($N = 132$) [Estrada et al., 2006]. These numbers suggest that resources or structural connectivity may not be sufficient in all cases to support primate populations or that people or stochastic events deter primates from using these habitats.

Changes in local and global market demands may result in changes in the distribution of agroforests and other agroecosystems where primate populations are able to exist. For example, the current trend to switch from shade coffee to sun coffee could result in a loss of important primate habitat, especially if one considers that of the 50 countries in the world with highest deforestation rates from 1990 to 1995, 37 were coffee producers [http://www.coffeehabitat.com/2006/02/the_problems˙wi/]. Similarly, the trend to expand cultivation of sun coffee at the expense of areas dedicated to shade cacao has similar consequences [FAO 2006; Rice & Greenberg, 2000]. In areas where cacao agroforestry systems have been abandoned due to disease problems (e.g. black pod rot, frosty pod rot caused by the pathogenic fungi (*Phytophthora* spp., http://www.ars.usda.gov/is/AR/archive/nov99/cacao1199.htm), plantations are converted to other land uses (e.g. pasture, banana, and oil palm production), which may have lower value for primate conservation.

While some primate populations are able to persist in agroecosystems, it is important to stress that this is no substitute for preserving primates in their natural habitats. However, the pressure of rapidly increasing human populations and the resultant demand for tropical resources is rapidly transforming primate habitats into mosaics dedicated to the production of food and other goods (e.g. palm oil for biodiesel). Globally, agroecosystems have a major presence in fragmented landscapes. At local and regional scales, well-managed agroecosystems have the potential to positively impact the long-term conservation of biodiversity, including that of primate taxa and populations, and must be considered in landscape-level approaches to conservation [Daily et al., 2003; Estrada et al., 2006; Murphy & Lovett-Doust, 2004; Ricketts 2001; Vandermeer, 2003]. Collaboration and cooperation from the landowners—who have become, unknowingly perhaps, important stakeholders in primate conservation—are key to the long-term persistence and success of primates in such landscapes.

Future Research Directions

Further research is necessary to conduct surveys and monitor primate populations in agroecosystems throughout the tropics. Studies of foraging ecology and population productivity will be useful to determine the relative success of primates in persisting in

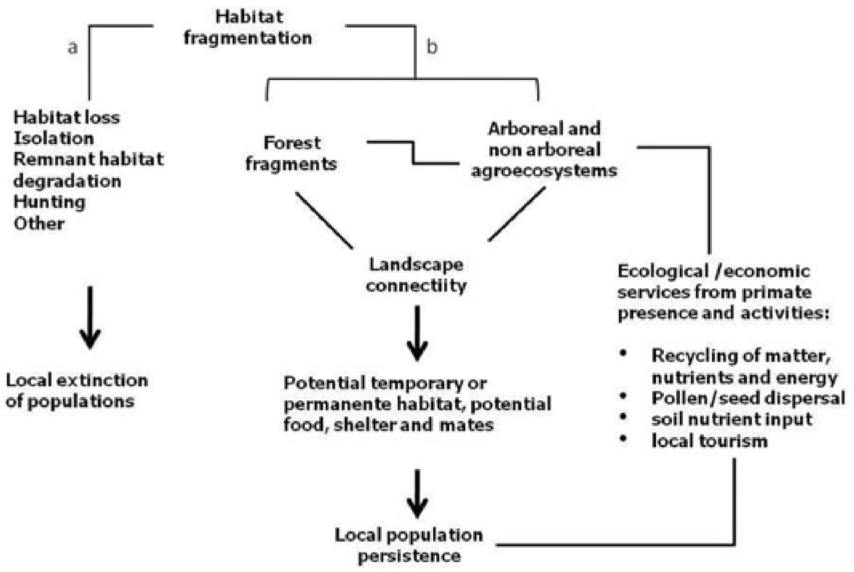

Fig. 1. Two sequences of human-induced habitat fragmentation leading to differing outcomes for primate persistence. Pathway "a" leads to extensive habitat loss, fragmentation, and isolation of remnant primate populations, with a rapid decline toward extinction. In this scenario, the landscape is mainly dominated by pasturelands. Pathway "b" consists of land use patterns in which forest fragments may coexist with different types of agroecosystems. Such conditions often allow primate populations to persist in the human-modified landscape.

agricultural landscapes. We also need to document variability in different types of agroecosystems and understand how primates respond to this variability, including determining the threshold levels of tree and forest cover leading to successful primate habitation. Assessments of landscape connectivity and development of methods to augment such connectivity to favor the medium and long-term persistence of primate populations using agroecosystems as temporary or permanent habitat are also of relevance (Fig. 1). Moreover, investigations determining the ecological and economic impact of primate presence and activities in the agroecosystems and the prevalence and outcome of human–primate interactions will be vital (Fig. 1). If the primates are agricultural pests, studies are necessary to evaluate how primate populations can be managed to decrease their negative impacts.

While our review has shown that many primate taxa are present in a large diversity of agroecosystems, not many studies exist that provide specific information on patterns of use and success of primate populations persisting over the long term in these habitats. In light of this, below we list several possible research priorities for the study of primates throughout tropical agroecosystems.

- Conduct landscape surveys of primate occupancy in agroecosystems.
- Assess density and population size of primate species occupying agroecosystems.
- Assess predation risks on primates in agroecosystems.
- Determine threshold levels for tree and vegetation cover to sustain primates within agroecosystems.
- Investigate the ecological and economic impact of primate presence and activities in agroecosystems and on their interactions with humans.
- Assess primate population management strategies to reduce conflict with humans.
- Assess impact of hunting on primates in agroecosystems.
- Assess risks of parasite and disease transmission in primate populations in agricultural landscapes and how to minimize these risks.
- Determine how landscape connectivity can be increased using agroecosystems to favor the medium- and long-term persistence of primate populations in agroecosystems.
- Assess the success of each primate taxa in human-altered habitats through studies of ecology and population productivity.

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in this article adhered to the American Society of Primatologists principles for the ethical treatment of primates.

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