

The Potential for Species Conservation in Tropical Secondary Forests

ROBIN L. CHAZDON,* CARLOS A. PERES,† DAISY DENT,‡ DOUGLAS SHEIL,§ ARIEL E. LUGO,** DAVID LAMB,†† NIGEL E. STORK,‡‡ AND SCOTT E. MILLER§§

*Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269-3043, U.S.A., email robin.chazdon@uconn.edu

†School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, United Kingdom

‡Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Panama

§Institute of Tropical Forest Conservation, Mbarara University of Science and Technology, P. O. Box 44, Kabale, Uganda

**International Institute of Tropical Forestry, USDA Forest Service, Ceiba 1201 Jardín Botánico Sur, Río Piedras, PR 00926-1119, Puerto Rico

††Center for Mined Land Rehabilitation, University of Queensland, Brisbane 4072, Queensland, Australia

‡‡Department of Resource Management and Geography, University of Melbourne, Melbourne, Australia

§§Smithsonian Institution, Washington, D.C. 20013-7012, U.S.A.

Abstract: *In the wake of widespread loss of old-growth forests throughout the tropics, secondary forests will likely play a growing role in the conservation of forest biodiversity. We considered a complex hierarchy of factors that interact in space and time to determine the conservation potential of tropical secondary forests. Beyond the characteristics of local forest patches, spatial and temporal landscape dynamics influence the establishment, species composition, and persistence of secondary forests. Prospects for conservation of old-growth species in secondary forests are maximized in regions where the ratio of secondary to old-growth forest area is relatively low, older secondary forests have persisted, anthropogenic disturbance after abandonment is relatively low, seed-dispersing fauna are present, and old-growth forests are close to abandoned sites. The conservation value of a secondary forest is expected to increase over time, as species arriving from remaining old-growth forest patches accumulate. Many studies are poorly replicated, which limits robust assessments of the number and abundance of old-growth species present in secondary forests. Older secondary forests are not often studied and few long-term studies are conducted in secondary forests. Available data indicate that both old-growth and second-growth forests are important to the persistence of forest species in tropical, human-modified landscapes.*

Keywords: forest biodiversity, habitat specialization, secondary forest, succession, tropical forest

El Potencial de Conservación de Especies en Bosques Tropicales Secundarios

Resumen: *A raíz de la pérdida generalizada de los bosques maduros en el trópico, los bosques secundarios probablemente jugarán un mayor papel en la conservación de la biodiversidad forestal. Consideramos una jerarquía compleja de factores que interactúan en el espacio y tiempo para determinar el potencial de conservación de los bosques tropicales secundarios. Más allá de las características de los fragmentos de bosque locales, la dinámica espacial y temporal del paisaje influye en el establecimiento, la composición de especies y la persistencia de bosques secundarios. Los prospectos para la conservación de especies primarias en los bosques secundarios se maximizan en regiones donde la proporción de superficie de bosque maduro-bosque secundario es relativamente baja, los bosques secundarios más viejos han persistido, la perturbación antropogénica después del abandono es relativamente baja, hay presencia de fauna dispersora de semillas y donde hay bosques primarios cerca de sitios abandonados. Se espera que el valor de conservación*

de un bosque secundario incrementa en el tiempo, a medida que se acumulan especies provenientes de los fragmentos de bosque primario remanentes. Muchos estudios están pobremente replicados, lo que impide evaluaciones robustas del número y abundancia de especies primarias presentes en bosques secundarios. Los bosques secundarios más viejos generalmente no son estudiados y son pocos los estudios a largo plazo en bosques secundarios. Los datos disponibles indican que tanto los bosques primarios como los secundarios son importantes para la persistencia de especies forestales en paisajes tropicales modificados por humanos.

Palabras Clave: especialización de hábitat, biodiversidad forestal, bosque secundario, bosque tropical, sucesión

Introduction

Throughout the tropics, secondary tropical forests are regrowing on abandoned agricultural land, following forest clearing, and in areas affected by large-scale natural disturbances, such as cyclonic activity and fire. Together, degraded old-growth forests (affected by road building, selective logging, recurrent fires, fragmentation, and overhunting) and secondary regrowth forests comprise roughly half of the world's remaining tropical forest (ITTO 2002). Despite the increasing area of secondary forests in many tropical countries (FAO 2007), their role in biodiversity conservation remains poorly understood. Wright and Muller-Landau (2006) contend that secondary forest regrowth may prevent mass extinctions in the tropics. They argue that expanding secondary forest may mitigate extinction caused by declining areas of old-growth habitat. Their conjecture led to debate on the potential for secondary forest to serve as a "safety net" for tropical biodiversity (Brook et al. 2006; Gardner et al. 2007; Laurance 2007). Many tropical species are threatened by a reduction in forest area, fragmentation, and degradation, but many others are resilient to changes in forest extent, quality, and the surrounding habitat matrix. Which species will find a safe haven in tropical secondary forests?

The potential for species conservation in tropical secondary forests cannot easily be determined by extrapolating from a small number of isolated studies and projected land-cover statistics. A complex hierarchy of factors interact in space and time to determine the conservation potential of tropical secondary forests within a broad regional context (Gardner et al. 2009). We examined how landscape and regional factors affect the conservation potential of secondary forests and present a brief synthesis of case studies. Although we focused on the occupancy of secondary forests by old-growth species, we recognize that secondary forests also provide critically important resources for wildlife (Parry et al. 2007), ecosystem services (Foley et al. 2007), and forest products (Chazdon & Coe 1999).

Secondary Forest

Second-growth, secondary forest, or regrowth forest can be defined in various ways, and these definitions have crit-

ical implications for assessing land-use change and for articulating conservation outcomes. The defining feature of secondary forest is discontinuity of forest cover (Corlett 1994). We adopted the comprehensive definition of the Food and Agriculture Organization (FAO 2003): forests regenerating largely through natural processes after significant disturbance of the original forest vegetation at a single point in time or over an extended period that display a major difference in forest structure or composition with respect to nearby primary forests on similar sites. Selectively logged old growth is not secondary forest, by our definition. Some ambiguities inevitably arise, particularly with regard to heavily logged old-growth forests, secondary forests enriched by planting trees and crops, and forests that have burned repeatedly over a short time interval (Barlow & Peres 2008). Forest structure and composition change gradually during succession, but at different rates (Chazdon et al. 2007). Structural features, rather than stand age, can be used to define successional stages (Arroyo-Mora et al. 2005).

Few remaining tropical forests can be considered primary forests, however (Willis et al. 2004). In many parts of the world, cyclones and landslides cause massive natural disturbance to tropical forests (Whitmore & Burslem 1988). Ecosystems in the cyclone and typhoon belts of the higher-latitude tropics (7–20° latitude) are often well adapted to these disturbances; forest vegetation quickly resprouts and rapidly regains structure and species composition (Burslem et al. 2000; Laidlaw et al. 2007). Similarly, a high proportion of species native to fire-adapted tropical dry forests can quickly recover from fires by resprouting (Pinard & Huffman 1997).

Habitat Specialization of Tropical Forest Species

Conservation efforts generally focus on species vulnerable to extinction, many of which are considered old-growth forest specialists. There is little purpose in assessing the potential for secondary forests to conserve only those species that—by definition—are restricted to or otherwise depend on old-growth forests. For our purposes, therefore, we assessed the potential for secondary forests to conserve any species occurring in old-growth forest (Table 1).

Assessing the potential for secondary forests to conserve tropical forest species requires detailed,

Table 1. Proportion of old-growth (OG) forest species recorded in secondary forests in studies examining the diversity of animal communities in tropical secondary (excluding selectively logged forest) and old-growth forests.*

<i>Taxa</i>	<i>Location</i>	<i>Forest age (years)</i>	<i>Number of species</i>	<i>Proportion OG species</i>	<i>Land use</i>	<i>Source</i>
Small mammals	Sri Lanka	old growth	8			Wijesinghe & Brooke 2005
		5	6	0.38	A	
Small mammals	China	old growth	5			Wu et al. 1996
		13	11	0.8	C	
Nonvolant mammals	Mexico	old growth	26			Estrada et al. 1994
		5-15	10	0.31	G	
		20-35	12	0.42	G	
Bats	Mexico	old growth	25			Castro-Luna et al. 2007
		3	23	0.72	S	
		8	16	0.6	S	
		30	25	0.84	S	
Primates	Sierra Leone	old growth	11			Fimbel 1994
		5-12	9	0.82	S	
Birds	India	old growth	86			Raman et al. 1998
		1	49	0.26	S	
		5	69	0.51	S	
		10	69	0.6	S	
		25	77	0.76	S	
		100	85	0.83	S	
Birds	Brazil	old growth	110			Borges 2007
		4-5	65	0.35	S	
		7-15	82	0.53	S	
		20-35	71	0.55	S	
Birds	Colombia	old growth	52			Andrade & Rubio-Torgler 1994
		<10	60	0.58	S	
		10-17	63	0.62	S	
Birds	Sulawesi, Indonesia	old growth	29			Sodhi et al. 2005
		40	28	0.86	C	
Birds	Brazil	old growth	144			Johns 1991
		5	154	0.66	A	
Birds	Costa Rica	old growth	167			Blake & Loiselle 2001
		4-13	132	0.5	G	
Anurans	Ivory Coast	old growth	20			Ernst & Rodel 2005
		25	18	0.75	P	
Anurans	Brazil	old growth	51			Tocher et al. 2002
		5-12	40	0.73	CB	
		12	41	0.69	C	
Anurans	Brazil	old growth	19			Souza et al. 2008
		4	8	0.32	C	
		15-20	13	0.37	S	
Anurans and lizards	India	old growth	31			Pawar et al. 2004
		1	10	0.26	S	
		5	7	0.16	S	
		10	11	0.29	S	
		35	19	0.61	S	
Lizards	Dominican Republic	old growth	11			Glor et al. 2001
		3	6	0.55	G	
		5	7	0.55	S	
		5-10	8	0.64	S	
		8	8	0.64	P	
Herpetofauna	Costa Rica	old growth	20			Heinen 1992
		5	17	0.55	P	
		25	19	0.6	P	
Ants	Australia	old growth	55			House et al. 2006
		4	33	0.36	AG	
		15	38	0.33	AG	
		20	31	0.33	AG	

continued

Table 1. (continued)

Taxa	Location	Forest age (years)	Number of species	Proportion OG species	Land use	Source
Ants	Brazil	old growth	39			Vasconcelos 1999
		1	10	0.26	A	
		10	37	0.72	G	
Butterflies	Ecuador	old growth	97			DeVries et al. 1997
		15–20	82	0.71	C	
		13	32	0.72	G	
Butterflies	Sulawesi, Indonesia	old growth	17			Veddeler et al. 2005
		5	13	0.47	S	
		15	18	0.71	S	
Dung beetles	Brazil	old growth	71			Quintero and Roslin 2005
		5	54	0.7	CB	
		10	58	0.8	CB	
Termites	Sumatra, Indonesia	old growth	34			Gillison et al. 2003
		13	23	0.59	C	
		17	56	0.73	C	
Trees, shrubs	Mexico	old growth	390			Castillo-Campos et al. 2008
Lianas and herbs		12–20	462	0.43	AG	
Trees (>4.8 cm dbh)	Brazil Antonina	old growth	51			Liebsch et al. 2008
		4	9	0.04	S	
		20	4	0.04	S	
Trees	Brazil Morretes	old growth	57			Liebsch et al. 2008
		15	24	0.19	S	
		25	37	0.44	S	
Trees (>2.5 cm dbh)	Brazil Cananeia/Iponanga	old growth	131			Liebsch et al. 2008
		15	31	0.09	S	
		15	39	0.15	S	
		25	29	0.1	S	
		36	53	0.19	S	
Trees (>10 cm dbh)	Costa Rica Chilamate	old growth	110			R.L.C., unpublished data
		11	53	0.25	G	
		11	48	0.15	G	
		24	63	0.22	G	
Tree Seedlings	Costa Rica Chilamate	old growth	69			R.L.C., unpublished data
		11	77	0.75	G	
		11	65	0.62	G	
Trees (>10 cm dbh)	Costa Rica La Selva	old growth	88			R.L.C., unpublished data
		21	45	0.26	G	
		29	64	0.36	G	
Tree Seedlings	Costa Rica La Selva	old growth	56			R.L.C., unpublished data
		21	47	0.66	G	
		29	46	0.59	G	

*Sampling methodologies were not standardized across studies. Land use prior to abandonment includes swidden (S), intensive agriculture (A), pasture (G), plantation (P), clearcut but not cultivated (C), and burned (B). References cited in the source column are provided in Supporting Information.

species-based inventory data over a wide range of forest conditions within tropical regions. To be useful, these assessments require consistent definitions of forest types across regions. Depending on the availability of a recorded or oral history, a forest can be considered old growth if there is no record of clearing, commercial timber harvesting, or other large-scale anthropogenic or natural disturbance in recent centuries. Old-growth species represent a broad continuum of resource and habitat requirements and life-history strategies. At one extreme are old-growth specialists that de-

pend on intact mature forest for specific dietary, behavioral, or establishment requirements. At the other extreme are ruderal species that thrive in naturally disturbed areas within old-growth forests, forest edge habitats, and second-growth forests after large-scale natural and human disturbance. Occupying all but the extremes of the continuum are generalists that require forest resources and habitats for survival and reproduction, but can occupy a range of forest types and disturbance regimes, potentially including young and old secondary forests. Generalist species are common components of the flora and fauna

in both secondary and old-growth forests (Barlow et al. 2007*a,b*; Norden et al. 2009). Classifications of species by habitat requirements are often tentative, given sampling limitations, available stand ages, and variation across regions. Moreover, presence and absence data cannot distinguish key from marginal habitats or source versus sink populations.

For many invertebrates local differences in microclimate and resource availability can diminish their diversity and abundance and alter overall community structure in secondary forests. Open canopies of early secondary forests may create suboptimal conditions at ground level for many invertebrates associated with old-growth forest floors (Didham et al. 1998). Secondary forests could be marginal habitat for many insect species that are less abundant there than in old-growth forests (Basset et al. 2008). Secondary forests are often dominated by species of ants that form ant mosaics. These ants prevent the occurrence of many other species of ants and other insects and enhance the abundance of sap-sucking insects that the ants tend (Blüthgen & Stork 2007). In Australian tropical rainforests, however, normal seasonal differences in the beetle fauna are greater than differences in the insect fauna before and after a major cyclonic disturbance (Grimbacher & Stork 2009).

Assessing Conservation Potential of Tropical Secondary Forests

Whether or not a species can find a safe haven in a tropical secondary forest depends on a nested set of factors and their complex interactions at multiple spatial and temporal scales. The persistence of regrowth forests within a region is linked with the region's socioeconomic and institutional determinants of land use and cover and their interactions with historical biogeography. Natural forest cover is expanding in some regions of the world and shrinking in others because of long-term climate change and changes in agricultural land use. Central African forests destroyed by a catastrophic climatic event approximately 2500 years ago are still expanding into adjacent savannas (Maley 2002), whereas recurrent fires are driving the conversion to secondary forest of vast tracts of seasonally dry Amazonian forests (Barlow & Peres 2008). Past eras of human settlement and indigenous forest management produced long-term legacies of species dominance and unique vegetation formations in many tropical regions (Gomez-Pompa & Bainbridge 1995; Bayliss-Smith et al. 2003; van Gernerden et al. 2003*a*). Moreover, many old-growth forests appear to be recovering from past disturbances (Chave et al. 2008). Thus, resilience of species assemblages to land-cover changes reflects past histories, evolutionary pressures, and previous extinctions (Balmford 1996). Although some forest

plant species may be able to persist as relic rootstocks, stems, or seeds in the soil following complete deforestation, most require persistence of secondary forest in the landscape and remnant patches of old-growth forests that serve as colonization sources.

Land-use history and the type and extent of forest clearance vary widely across landscapes and strongly affect the nature, rate, and heterogeneity of secondary regrowth (Chazdon 2003). The degree of burning prior to and after pasture abandonment strongly affects successional pathways in Central Amazonia (Mesquita et al. 2001). In pasture landscapes of the Neotropics, remnant trees left during pasture establishment can enhance secondary forest regeneration by attracting vertebrate frugivores (Guevara & Laborde 1993). In shifting cultivation landscape mosaics, individual fallows contain few species characteristic of old-growth forest, but heterogeneity among fallows contributes strongly to landscape diversity (Finegan & Nasi 2004).

Species Conservation in Secondary Forests in a Landscape Context

The spatial and temporal dynamics of the landscape influence initial establishment of secondary forest patches, their changing species composition, and their persistence. These landscape-level dynamics influence patch age, longevity, development, and spatial distribution (Arroyo-Mora et al. 2005). Long-term persistence of secondary forest patches is essential for regeneration of long-lived taxa, such as slow-growing canopy and emergent trees (Liesch et al. 2008). Areas remote from seed sources show poor development of secondary vegetation, low species richness, and few old-growth species (Thomlinson et al. 1996). Furthermore, areas that have been disturbed chronically and intensively (e.g., burn frequently) show poor forest regeneration and low rates of biomass accumulation (Zarin et al. 2005). In contrast, regrowth areas that are close to old-growth source populations or that are connected to intact forests through forested corridors are more likely to contain a rich assemblage of forest species (Lees & Peres 2008*a*). At La Selva Biological Station, Costa Rica, secondary forests contain high species richness of birds and trees that colonize from nearby old-growth areas (Blake & Loiselle 2001; Norden et al. 2009).

The age distribution of secondary forests within a landscape is affected by rates of land abandonment and rates of clearing of regrowth forests. Globally, nearly 70% of reported long-term forest regeneration is in hilly, upland, and mountainous environments that are considered marginal for large-scale agriculture and ranching (Asner et al. 2009 [this issue]). Agricultural abandonment is more likely in areas of marginal value for agriculture (Rudel

et al. 2000; Arroyo-Mora et al. 2005). Young secondary forests tend to have higher rates of clearance than older secondary forests. The probability of clearing is negatively related to secondary forest age in four lowland landscapes of Colombia (Etter et al. 2005). Forests <10 years old are more likely to be cleared for land development in Puerto Rico than older age classes of second growth (Helmer et al. 2008). In the lower Mekong Basin, deforestation rates were three times higher in secondary forests than in dense (presumably old-growth) forest from 1993 to 1997 (Heinimann et al. 2007). In Indonesia secondary forests and heavily logged forests are the most likely forest types to be converted to oil-palm monocultures (Fitzherbert et al. 2008). Soils, topography, road access, and proximity to urban areas further affect persistence of second-growth forests. Older secondary forests in Puerto Rico are more likely to persist on limestone substrates, at higher elevations, on steep slopes, farther from roads, and in areas with less surrounding pasture (Helmer et al. 2008).

Clearing of young secondary forests has several implications for conservation: the future extent of secondary forest cover is compromised, including potential biological corridors and buffer zones; the average age and state of maturity of secondary forest in a landscape advances slowly or plateaus; and older forest patches are more likely to persist to full maturity than surrounding younger forest patches, but may become more isolated. Long-lived species that colonize early stages of regrowth may be lost. We speculate that a more balanced age structure of mature and secondary forest patches maximizes overall conservation opportunities for old-growth species within fragmented and largely deforested landscapes and increases species richness at the landscape scale.

Species Conservation in Secondary Forests in a Regional Context

At the regional level, biodiversity and its conservation are contingent on history, geography, and the political, social, and economic context. Moreover, the fate of biodiversity in human-modified landscapes depends strongly on areas managed for agriculture and forestry (Harvey et al. 2008). Due largely to these regional differences, case studies present stark contrasts in the role secondary forests play in safeguarding forest species. For example, secondary forests in Hong Kong, Singapore, and densely settled parts of Brazil are regrowing within an increasingly urbanized matrix, where little or no original forest remains (Baitello & Aguiar 1982; Turner et al. 1997; Zhuang & Corlett 1997). In these cases secondary forests provide critical refugia for remaining forest species.

Regional land-use dynamics affect the potential for conserving old-growth species in secondary forests. At one

extreme are regions dominated by shifting cultivation or smallholder agriculture, where the ratio of secondary to old-growth forest area is relatively low. These regions tend to have a high fraction of land area in forest cover, even in cases where human settlement and farming have occurred for centuries. Anthropogenic disturbance after abandonment is relatively low, availability of seed dispersal agents is usually high, old-growth forests are close to abandoned areas, and forest patches have high connectivity (Finegan & Nasi 2004). All these factors favor high rates of dispersal and colonization of forest species and therefore contribute to rapid species accumulation in secondary forests (e.g., Finegan & Nasi 2004; Vulinec et al. 2006). Moreover, traditional management practices enhance fallow succession and favor species that catalyze forest regrowth (Diemont et al. 2006). A wide range of secondary forest ages and stages coexist within these landscapes, providing heterogeneous habitats and maximizing biodiversity conservation at the landscape scale. Patches of old secondary forest (>40 years old) that remain in these regions often play an important role in conservation of forest species (Sodhi et al. 2007; Urquiza-Haas et al. 2009). Intensification by shortening of fallow cycles during shifting cultivation, however, limits species accumulation in secondary forests (Lucas et al. 1993; Neff et al. 2006). Furthermore, increasing the number of fallow cycles can compromise soil fertility and regrowth potential (Lawrence 2004).

At the other extreme are regions with a history of large-scale deforestation or industrialized agriculture, where most remaining forest patches are second growth. Under these conditions, old-growth species are threatened due to forest loss, degradation, and fragmentation, and poor forest regrowth in abandoned areas. Second-growth patches tend to be very young, with a high probability of clearance outside protected areas. Old-growth forest patches are scarce, and the intervening matrix restricts animal movement. These factors reduce populations of seed-dispersing animals, which limit the dispersal of large-seeded tree species. Consequently, the rate of species influx into secondary forest patches is low. For example, only one-third of the 268 tree species occurring in a 200-ha primary forest remnant of the Zona Bragantina of northeastern Amazonia exist in neighboring secondary forest patches (Vieira 1996). This is the oldest Amazonian deforestation frontier, and virtually all remaining forest cover is second growth.

Most tropical landscapes occupy an intermediate position between these two extremes and have different degrees of spatial and temporal dynamics. The proportion of total forest cover in secondary forest is usually low in recent deforestation frontier zones, but existing secondary forests are dominated by very young stands. Helmer et al. (2009) estimated secondary forest age and biomass accumulation across a landscape in Rondônia, Brazil (1975–2003). In 2003, 65% of the secondary forest

was <5 years old, whereas only 9.8% was 19–28 years old, but 89% of the forest cover in the study region was classified as old-growth forest (Helmer et al. 2009). In lowland regions of Colombia that are still undergoing forest clearing, little secondary vegetation has regenerated, which has created a gap in the spatial mosaic of successional habitats within the landscape (Etter et al. 2005). Apart from the “old” deforestation frontier in northeastern Amazonia, secondary forests in Amazonia are generally concentrated along deforestation fronts, peak in total cover at around 50% deforestation and then decline in extent as deforestation becomes more complete (Neef et al. 2006). In regions that have undergone a forest transition (Rudel et al. 2005), secondary forest patches increase in age and spatial extent and may provide stable habitats for old-growth species. For example, the Sarapiquí region of Costa Rica is undergoing landscape-level forest recovery as secondary forests regrow and are protected (Read et al. 2001).

Species Assemblages During Forest Regrowth

In countries and regions that have undergone forest transitions and are now showing net increases in forest cover, regrowth forests are developing under a new set of conditions. In Puerto Rico nearly complete forest clearing for agriculture followed European settlement centuries ago. Economic policies favored abandonment of agriculture in the 1940s, and forest cover increased from 18% in 1951 to 45% in 2000 (Helmer et al. 2008). Currently, 78% of Puerto Rico’s forest is <50 years old (Helmer et al. 2008). In the process of forest regrowth, mixing of native and alien tree species has led to altered community composition (Lugo & Helmer 2004; Lugo & Brandeis 2005). With time, however, native species are regenerating and alien species are declining (Lugo & Helmer 2004).

Novel forests can also emerge from deliberate enrichment of secondary forests with species with subsistence or commercial value, such as fruit or nut trees, or species that produce gums or resins, medicinal plants, and timber trees (Lamb 1969; Ådjers et al. 1995). Secondary forest enrichment has been especially common in parts of the Asia-Pacific region and in Mayan forests of Mesoamerica. These forests have been referred to as agroforests, improved fallows, and or forest gardens (Clarke & Thaman 1993; Michon 2005; Diemont et al. 2006).

Successional Trajectories and Compositional Change

Like a good Bordeaux, the value of a secondary forest is expected to increase over time, as species from remaining old-growth forest patches move in and accumulate.

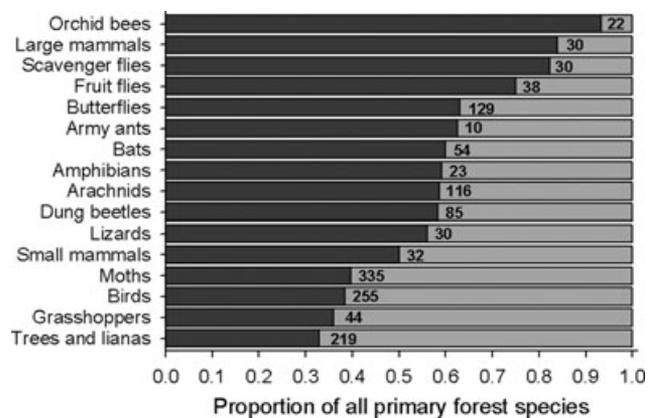


Figure 1. Proportion of primary forest species (genera for trees and lianas) recorded in 14- to 19-year-old secondary forests across 16 taxonomic groups of plants, invertebrates, and vertebrates sampled throughout the Jari forest landscape of northeastern Brazilian Amazonia (data from C.A. Peres, J. Barlow, T.A. Gardner, and the Jari Forest Project database; see Barlow et al. [2007a] for further details). Numbers in gray bars are the total number of species or genera for each taxon.

Although typical old-growth species and endemic forest specialists may be missing from young stages of forest regrowth, they may be able to establish later. Assessments of conservation value therefore depend on secondary forest age. Successional trajectories are also affected strongly by initial conditions and the surrounding landscape (Chazdon 2003, 2008b). In the lower Guinea region of South Cameroon, the proportion of endemic species increases with age of shifting cultivation fallows (van Gemerden et al. 2003b). In Atlantic forest of southern Bahia, Brazil, the percentage of old-growth tree species in secondary forests increased from 12% in 10-year-old stands to 42% in 40-year-old stands (Piotto et al. 2009). Small abandoned agricultural plots (4–67 years old) embedded within a large remnant old-growth fragment in the Brazilian Atlantic forest gradually accumulated old-growth tree species over time, but old-growth forest plots were still at least twice as species rich as even the oldest regrowth plots (Santos et al. 2007).

In the most comprehensive assessment to date of the conservation value of tropical secondary forests, Barlow et al. (2007a) compared 15 taxonomic groups in terms of the proportion of old-growth species in 14- to 19-year-old second growth and in plantation forests in the Jari Forestry project in the Brazilian Amazon. Overall, they found that secondary forests hold 59% of the old-growth species, but different taxa show idiosyncratic responses to land-use change (Fig. 1). Whereas 95% of the old-growth orchid bee species are found in second-growth, fewer than 40% of old-growth tree and liana genera occur

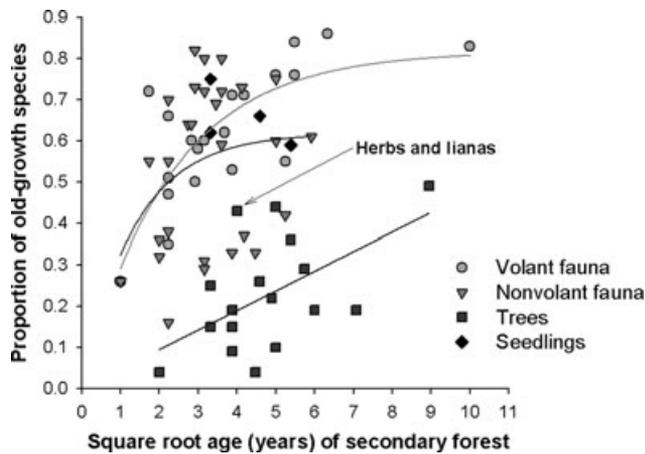


Figure 2. Successional influx of different taxa into secondary forests of different ages. Data were derived from studies listed in Table 1. In each case, we determined the proportion of old-growth species that occurred in each second-growth area sampled. Curves for trend lines were fit with a positive exponential function. No trend line was fit for seedlings, which only have four data points.

there (Fig. 1). These results reflect a best-case scenario because of the largely intact nature of the primary-forest matrix surrounding secondary forests and the vertical stratification of a range of sampling techniques used, which may have underestimated the species richness of several arthropod taxa in primary forests. Yet the secondary forests examined were relatively young and will likely accumulate many species over time—if they persist.

In the absence of long-term studies over decades or centuries within particular areas, one can gain insights into changes in species composition during secondary regrowth by comparing the proportion of old-growth species in second-growth areas of different age within and across tropical regions (Table 1). Conservation potential in secondary forests varies widely because of landscape and regional influences. For many taxa and locations, the proportion of old-growth species increases with secondary forest age, which suggests a gradual influx of old-growth species over time (Fig. 2). Available data reflect a sampling bias toward young secondary forests and likely underestimate the current and future potential for conservation of old-growth species in later stages of succession (Table 1). Volant invertebrates and vertebrates (butterflies, birds, and bats) are often highly adept at crossing wide gaps (Lees & Peres 2009) and typically show the highest rates of successional influx, which reflects the higher vagility of these taxa. Nevertheless, some species and guilds of birds, such as understory insectivores, are highly reticent to cross gaps, highways, or other linear habitat barriers (Laurance et al. 2004). Less than half of the old-growth species of nonflying mam-

mals occur in secondary forests in Mexico (Estrada et al. 1994). Recovery of animal taxa is also likely to depend on recovery of vegetation (Dunn 2004). Bird communities tracked the recovery of vegetation during succession following shifting cultivation in India; the proportion of old-growth species increased from 0.26 in a 1-year-old fallow to 0.83 in a 100-year-old secondary forest (Raman et al. 1998; Table 1).

Limited data further suggest that animals have higher proportions of old-growth species in secondary forests (0.33–0.86) compared with trees ≥ 10 cm dbh (diameter breast height) (0.04–0.44; Table 1), as was also observed in the Jarí landscape (Barlow et al. 2007a; Fig. 2). Larger trees (≥ 10 cm dbh), in particular, show a low proportion of old-growth species (0.15–0.36), even under “ideal” conditions of protected secondary forests adjacent to large tracts of old-growth forest in Costa Rica (Table 1; Letcher & Chazdon 2009). A more encouraging picture emerges when tree seedlings are compared, however. There is a 2- to 3-fold increase in the proportion of old-growth tree species in the seedling layer (Table 1, Fig. 1; Norden et al. 2009). During succession, species richness accumulates more rapidly for species with small stems (Chazdon 2008b). After initial canopy closure, slow-growing seedlings require decades or longer to become trees, imposing a considerable time lag before these species are observed in tree surveys or reach reproductive maturity.

Successional trajectories may fail to converge on old-growth composition for a variety of reasons (Ewel 1980; Chazdon 2003). Many large-seeded tree species characteristic of old-growth forests in Singapore have failed to regenerate in secondary forests due to local extinction of frugivorous birds and bats that disperse their seeds (Corlett 1992; Lane et al. 2006). Yet, conservation of forest species, including endemics, can still be effective even in the absence of complete recovery to the “original” forest composition (Lugo & Helmer 2004). Generalist tree species can also serve as “nurse” species or as food sources, nest sites, and roosting sites for other species (Martinez-Garza & Howe 2003).

Knowledge Gaps

Characterization of the complex relationships that determine the potential for species conservation in tropical regrowth forests has just begun. Much more information is needed on species abundance, metapopulations, landscape dynamics, dispersal, and movement in old-growth, second-growth, and matrix habitats for a wide range of stand ages and land-use histories and across many different taxa (Bowen et al. 2007; Chazdon et al. 2009). Studies that integrate multiple spatial scales are particularly needed. Much of the information available is from

small, poorly replicated samples that provide insufficient data to characterize distributions of rare species or to assess the number and abundance of old-growth species present in secondary forests. Intra-annual variation can have a significant effect on conclusions drawn from studies in which secondary forests and old-growth forests are compared (Barlow et al. 2007*b*). Intermediate and older secondary forests (> 10 years) are especially understudied, contributing to uncertainties regarding rates and mechanisms of successional influx. The results of studies on species distributions in different forest types are also strongly affected by the spatial scale of the study (Hill & Hamer 2004). Moreover, with the exception of a few long-term vegetation studies (Chazdon et al. 2007), taxonomically based inventories are generally conducted once and chronosequence predictions are untested.

Shifting baselines of biodiversity patterns in remaining old-growth forests pose further challenges to comparing conservation value in secondary forests across taxa and regions (Gardner et al. 2009). The processes of disturbance and recovery that led to the initial development of secondary forest may have major implications for the persistence and recovery of forest vegetation, yet these factors, which are often spatially irregular, have not been evaluated well at sufficiently large scales (Rudel et al. 2009 [this issue]).

Replicated, long-term, and landscape-level studies are also critically needed to reveal the spatial distribution and dynamics of mature and secondary forest patches. Combining multivariate remote-sensing data with biodiversity inventories will help elucidate linkages between landscape structure and current and future conservation potential.

Enhancing Species Conservation in Regrowth Forests

Beyond protecting existing old growth, conservation policies should recognize and build on the role of regrowth and other nonpristine habitats at the landscape level (Harvey et al. 2008). First, secondary forests of all ages should be protected. Older, more species-rich secondary forests near protected areas should be the highest priorities. Investing in protection of young secondary forests promises big dividends over time. Conservation easements and payments for environmental services can, under appropriate circumstances, provide incentives for protecting secondary forests on private lands. Second, opportunities should be sought to expand secondary forest buffer zones surrounding old-growth forests and riparian zones and to use these to develop links to other reserves through biological corridors. Biological corridors consisting of existing forest remnants and agroforestry plantations should be planned to optimize the potential for diverse secondary regrowth (Harvey et al.

2008). Third, areas where regeneration is slow or inhibited should be priorities for assisted regeneration, reforestation, agroforestry, or sustainable agriculture (Lamb et al. 2005; Chazdon 2008*a*). Fourth, monitoring and public-education programs should be developed to enable adaptive management practices wherever successional trajectories diverge into unfavorable pathways (e.g., to prevent the early spread of invasive species).

Few of these actions will be successful in the long term unless institutions and policies allow rural people to benefit in some way from the protection of secondary forests (Chazdon 2008*a*). Active participation of local people may involve recognition of customary ownership rights over these forests, payments for carbon storage or other ecosystem services, or encouraging management of these forests to enhance their long-term economic and conservation value (Harvey et al. 2008). Involving local people in the management of forests increases the likelihood that secondary forests will persist. Active management may also require some trade-offs between conserving biodiversity and enhancing subsistence or commercial productivity. Throughout much of the tropics, secondary forests can provide a safe haven for many wild species, but they need our sustained help to fulfill their potential.

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Supporting Information

References cited in the source column in Table 1 are available as part of the on-line article (Appendix S1). The author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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