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Changes in vegetation structure and composition along a tropical forest chronosequence: implications for wildlife

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Abstract

Changes in tropical forest structure and species composition that occur during regeneration following land abandonment may have important consequences for wildlife populations. Many animals rely on forest resources as sites for foraging, nesting, and protection that may vary in abundance in forests of different ages. In this study, we examined aspects of forest composition and structure thought to be important to wildlife along a tropical moist forest chronosequence in the Barro Colorado Nature Monument (BCNM) of central Panama. Secondary forests of approximately 20, 40, 70, and 100 years in fallow as well as two stands of old-growth forest (>500 years) were intensively studied. All stands were located on relatively fertile soils and were in close proximity to old-growth forest. Within 70 years following cessation of active management, many structural aspects of secondary forests resembled those of old-growth stands. Large living tree (≥ 65 cm diameter) density and coarse-woody debris volume increased with secondary forest age and were equivalent to old-growth levels by 70 years. Snag density and basal area did not differ with stand age. Species composition and availability of food resources in secondary forests did not converge on old-growth characteristics as quickly as most structural aspects, but many resources available to generalist frugivores were common across the chronosequence. Tree, but not liana, species composition of secondary stands became more similar to old growth with increasing forest age. Understory fleshy fruit availability was highest in young secondary stands, while importance values of trees and lianas with animal-dispersed fruits remained unchanged across the chronosequence. The importance of species particularly important to some frugivores, such as *Ficus* and *Virola*, had unpredictable distributions, but palm importance value increased with stand age. We suggest that young secondary forests may provide adequate nesting, foraging, and roosting resources for many animal taxa, but some populations of animals specializing on coarse-woody debris, large trees, or particular species of trees may be limited in secondary forest less than 70 years old.

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1. Introduction

Old-growth tropical forests are high priorities for conservation because of their complex structure and

high tree and animal species diversity. However, the conservation value of secondary tropical forests also becomes important as old-growth tropical forests are logged or cleared. Without further anthropogenic disturbance, natural successional processes eventually may restore attributes of old-growth forests to these degraded ecosystems. Although the relative roles of vegetation structure and composition in structuring

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faunal communities are not clear (Crome and Richards, 1988; MacNally, 1990; Bersier and Meyer, 1994, 1995; Adler, 2000), secondary forest vegetation can provide important resources for nesting, foraging, and protection for a variety of animal taxa. Indeed, logged or secondary forests often exhibit higher animal diversity than old-growth forests (Hamer et al., 1997; Aleixo, 1999). In addition, many insect species that rely on larval host plants in tropical forest understory also visit floral resources in early successional areas, highlighting that animal life cycles can be complex and include reliance on plant resources found in several successional patch types (Gilbert, 1980). On the other hand, populations of specialists and endemic or localized species often are missing from regenerating forests (Johns, 1988; Hill et al., 1995; Aleixo, 1999). The changes in forest structure and composition that occur after land abandonment may have different implications for different wildlife populations.

In tropical moist forest climates, secondary succession from pasture, plantations, or agriculture proceeds rapidly with some ecosystem characteristics converging on old-growth forest patterns within a few years of regrowth (Guariguata and Ostertag, 2001). For example, leaf area index (Uhl and Jordan, 1984), soil nutrient processes (Reiners et al., 1994; Hughes et al., 1999), and standing leaf litter mass (Denslow and Guzman, 2000) in young forests (<40 years) differ little from values of old secondary or old-growth forests. Other aspects of wildlife habitat and food resources may develop only many years following cessation of management. The suitability of secondary forest as wildlife habitat likely varies as a function of forest age and land-use history, as well as the animal species in question.

Many of the forest resources utilized by specialist and generalist animals are quantifiable forest structural characteristics that can be examined in different aged forests. Dead and mature trees are used by birds and mammals for roosting, foraging, drumming, and perching (Hamilton and Whitaker, 1979; Gibbs et al., 1993; Pattanavibool and Edge, 1996; Styring and Ickes, 2001). The population sizes of at least one tropical cavity-nesting bird, the Puerto Rican parrot (*Amazona vittata*), are limited by a lack of large, old trees (Snyder et al., 1987). Populations of the arboreal lemuroid ringtail possum, *Hemibelideus lemuroids*,

which is endemic to the upland tropical rainforests of north Queensland, Australia, also likely are limited by available tree cavities in old-growth rainforests (Laurance, 1990). Downed coarse-woody debris (DCWD) provides a specialized resource for shelter, nesting, and foraging for some amphibians and reptiles (Whiles and Grubaugh, 1993; Hecnar, 1994), small mammals (Hamilton and Whitaker, 1979; McCay, 2000), and invertebrates (Seastedt et al., 1989) in temperate forests of the eastern United States. In tropical forests, downed dead wood is also important for foraging and nesting of termites (Eggleton et al., 1997; Dangerfield and Schuurman, 2000) and bivouacking by army ants (Roberts et al., 2000).

Plant species composition may also affect habitat quality for some animal taxa. The abundance of fleshy fruits may affect densities of generalist frugivores (Sorensen and Fedigan, 2000; Stevenson, 2001), and some taxa such as *Ficus* and some palm species may be critical resources for many species of birds and mammals during periods of fruit scarcity (Glanz et al., 1982; Terborgh, 1986; Windsor et al., 1989; Forget et al., 1994). In Panama, spiny rat reproduction rates and population densities are strongly related to fig and palm fruit availability (Adler, 1998, 2000). *Virola* species (Myristicaceae) are significant food sources for a subset of larger frugivorous birds, such as toucans and tityras, and have protracted fruiting seasons (Howe, 1981; Howe and Vande Kerchove, 1981). Thus, the abundance of fleshy-fruited plants, as well as some other pivotal species, is an indicator of habitat quality for a variety of frugivores.

In this study, we examined several structural and compositional aspects of forest habitats known to be important to wildlife along a tropical forest chronosequence in central Panama. Although specific habitat requirements will vary among animal taxa, a number of forest structural and floristic characteristics likely have broad implications for habitat quality for many different species of wildlife. In particular, we compared stands of different ages with respect to the density of large living and dead trees and understory plants, volume of downed coarse-woody debris, species composition, and the importance of fleshy-fruited species. We also quantified the importance of several keystone plant species used by many generalist animals as well as some plant species pivotal to the abundance of particular specialists along the chronosequence.

2. Methods

2.1. Study area

Study stands were located in Panama within the Barro Colorado Nature Monument. The Barro Colorado Nature Monument (BCNM) comprises Barro Colorado Island (BCI, 9°10'N, 79°51'W), a research station of the Smithsonian Tropical Research Institute, as well as several adjacent mainland peninsulas. The area receives approximately 2600 mm of rainfall annually, predominantly during the 7-month wet season from May through December (Windsor, 1990). Soils of the BCNM are Oxisols and Alfisols, both high in nitrogen and phosphorus availability (Yavitt, 2000). The vegetation is classified under the Holdridge life zone system as tropical moist forest (Holdridge and Budowski, 1956). Canopy height reaches ca. 30 m with emergent trees approaching 50 m (Knight, 1975). The canopy of the old-growth forest is dominated by emergent trees in the Leguminosae and Bombacaceae. Smaller-stature trees such as *Cordia alliodora* (Boraginaceae), *Spondias mombin* (Anacardiaceae), *Annona spraguei* (Annonaceae), and *Miconia argentea* (Melastomataceae) are common in secondary forests (Denslow, unpublished data). Descriptions of the forest composition and structure on BCI are found in Foster and Brokaw (1982), Croat (1978), Hubbell and Foster (1990), and Denslow and Guzman (2000).

Old-growth forest occupies about half of BCI (Foster and Brokaw, 1982) and small areas at the bases of the mainland peninsulas of Gigante and Bohio. Portions of the area now included within the BCNM were used to pasture dairy cattle and to produce fruits and vegetables between the 1880s and the establishment of the Nature Monument in 1979. Detailed accounts of land-use history of the BCNM are provided by Leigh (1996) and Denslow and Guzman (2000). Today the BCNM is a patchwork of old-growth and secondary forests of different ages.

2.2. Stand selection

Eight stands were selected for intensive study. They represent two replicates each of secondary forests of approximately 20, 40, 70, and 100 years in fallow as well as two stands of old-growth forest (>500 years). Study stands were at least 5 ha in size on relatively

level topography and had not been subject to subsequent human disturbance once fallowed. They are representative of stands of similar ages and histories in the BCNM. Stand ages were estimated using historical records, aerial photographs, and interviews with longtime residents (see Denslow and Guzman, 2000 for details). There is no indication that the old-growth forests have ever been logged or cultivated (Piperno, 1990). Further descriptions of the forest history, soil properties, light availability, and geographic locations of the stands can be found in Denslow and Guzman (2000).

2.3. Vegetation sampling

In nine of the 10 sites, vegetation was sampled in two parallel 160 m × 10 m transects composed of contiguous nested quadrats. Transects were located well inside forest edges and were separated by at least 20 m. The configuration of one 20-year-old site (Saino) was sufficient only for the establishment of a single transect, which was interrupted in two places by creeks. We used a nested sampling design to sample different forms of vegetation. In each transect except Saino, we identified and measured the diameter at breast height (dbh) of trees (≥5 cm dbh) in 16 contiguous quadrats (10 m × 10 m; total of 3200 m² per stand); we counted and identified understory vegetation (large herbs, shrubs, saplings, and treelets ≥1 m tall and <5 cm dbh) in 32 quadrats (5 m × 5 m; total of 1600 m²); and we identified and measured all rooted lianas ≥0.5 cm diameter at their thickest point if growing horizontally, or at 1.3 m above the ground if growing only vertically, in 8 quadrats (5 m × 10 m; total of 800 m²). In the sole transect at Saino, we measured trees in 13 quadrats (1300 m²), understory vegetation in 27 quadrats (675 m²), and lianas in 8 quadrats (400 m²).

2.4. Coarse-woody debris sampling

We measured standing dead trees (hereafter called snags) and downed coarse-woody debris (e.g. boles and branches; hereafter called DCWD) in sixteen 5 m radius circular quadrats, each nested within the 10 m × 10 m quadrat used for the tree sampling. A total area of 1256 m² was sampled per stand. For the Saino site, thirteen 5 m radius circular quadrats were sampled for a total area of 1021 m². The length of each

piece of DCWD was measured to the nearest cm. In addition, we either categorized each piece to one of two diameter classes (5–10 cm or 10–15 cm) or measured the diameter at the midpoint for downed pieces >15 cm in diameter. Volume of DCWD was estimated as a cylinder using the midpoint diameter and length. The level of decay of each piece of DCWD was evaluated using the three-class system of Stewart and Burrows (1994): (1) structurally intact; (2) structurally weakening; and (3) advanced stage of decay. In addition, we measured the dbh of all snags ≥ 5 cm dbh and calculated their basal area.

2.5. Data analysis

We used similarity in species' relative density (percent total stand density) between secondary stands of each age and the old-growth stands as an estimate of the degree of convergence on old-growth species composition. Pairwise stand similarities were calculated as Sørensen's Similarity Index (SSI) based on relative density of tree and liana species that occurred in at least two stands.

We examined the distribution of species properties across the chronosequence based on species importance values (IV) in the stands. The IV for each species per stand was calculated as the sum of relative density (number of individuals of a species/total number of individuals in the stand) and relative dominance (total basal area of the species/total basal area of all individuals in the stand) (cf. Curtis and Cottam, 1962). We felt that the impact of a species on the forest as a whole would be better approximated by this measure than by density or basal area alone. The results using IV and total basal area were very similar. For generalist frugivores, the density and basal area of endozoochorous trees can be used as rough estimates of fruit production (cf. Adler and Kielpinski, 2000). Thus, we use IV as an estimate of fruiting volume for particular species.

We assessed the distribution of fruit production by several different indices. Tree and liana species were classified as wind or animal dispersed as indicated in species descriptions by Croat (1978), and the total IV of each dispersal type was calculated. Only the most important liana species up to a cumulative IV of 150 out of 200 were used because there were many unidentified lianas for which dispersal syndromes could not be assigned. Almost all tree species were identified

and, therefore, all tree species were used for dispersal classification. Average propagule size for each bird-dispersed tree species was determined by reference to Croat (1978). Propagule size was either the maximum fruit diameter for fruits eaten whole or the seed diameter for fruits that split to expose seeds with arils. Species were classified into two propagule diameter classes: small (0.1–1.2 cm) and large (>1.2 cm), chosen to reflect the size of propagules eaten by small birds (gapes ≤ 1.2 cm), such as manakins, flycatchers, thrushes, and tanagers, and by large birds (gapes 1.2–3.5 cm), such as toucans, guans, chachalacas, and trogons (Wheelwright et al., 1984). Finally, density of all understory trees and shrubs that produce animal-dispersed seeds was calculated per stand.

Importance values were also used to assess the distribution and abundance of three groups that produce significant sources of fruit for animals on the BCNM (*Ficus*, *Virola*, and palms) and woody species whose leaves are used by the tent-making bat *Uroderma bilobatum* (Chiroptera: Phyllostomidae; Choe, 1994; Kunz et al., 1994).

Stand structural characteristics were compared by pooling data from quadrats and transects by stand, and the stand was used as the replication unit for each age class. Analyses were performed with SAS for Windows Version 8 (SAS Institute, 2000). Trends among the secondary stands were examined using regression (PROC REG) of stand properties on forest age, which was \log_{10} transformed for all analyses. Stand properties thus compared included volume of DCWD; snag density and total basal area; IVs of wind or animal-dispersed trees and lianas; density of fleshy-fruited understory plants; and IVs of large- and small-seeded bird-dispersed trees, important fruit producers (*Ficus*, *Virola*, palm trees), and trees used by tent-making bats. Analysis of covariance (ANCOVA) was used to examine whether there were different patterns across stand age in volume of DCWD of different size and decay classes as well as basal area of snags of different size classes.

3. Results

3.1. Vegetation structure

The similarity between secondary and old-growth forest structure was greatest in stands at least 70 years

Table 1
Number of trees per hectare in dbh size classes based on sampling 3200 m² per age in two stands each of secondary and old-growth forest in the Barro Colorado Nature Monument

Diameter at breast height (cm)	Approximate forest age (years)				
	20	40	70	100	OG
5–15	1078	761	667	1047	1122
15–25	182	172	141	89	105
25–35	56	95	39	52	63
35–45	9	27	36	42	27
45–55	13	8	23	16	11
55–65	7	3	6	8	8
≥65	0	3	22	17	8

Only 1300 m² were sampled for one of the 20 years stands; OG, old-growth forest.

in fallow. Large trees were absent from 20-year-old stands and uncommon in 40-year-old stands whereas the 70 and 100-year-old stands had similar number of trees in each dbh size class as old growth (Table 1). Understory vegetation was most dense in the young secondary forest and declined with forest age (Fig. 1). In old-growth forest, understory densities were similar to those in 70-year-old secondary forest stands.

The volume of DCWD increased with secondary stand age and was highest in old growth (Fig. 2a). We estimated mean volume of DCWD (\pm S.D.) in old-growth stands at approximately 35 m³/ha \pm 1.4 m³/ha,

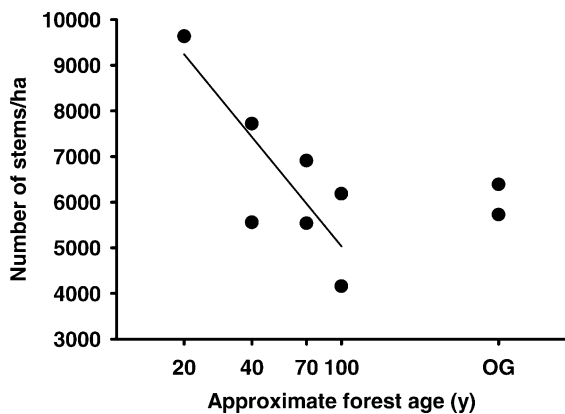


Fig. 1. Number of shrub and sapling stems ≥ 1 m and < 5 cm dbh of secondary and old-growth (OG) tropical forest stands in central Panama ($P = 0.006$, $r^2 = 0.74$). Each point represents one stand. Points for the 20-year-old forest stands are on top of each other. Stand age is plotted on a log scale.

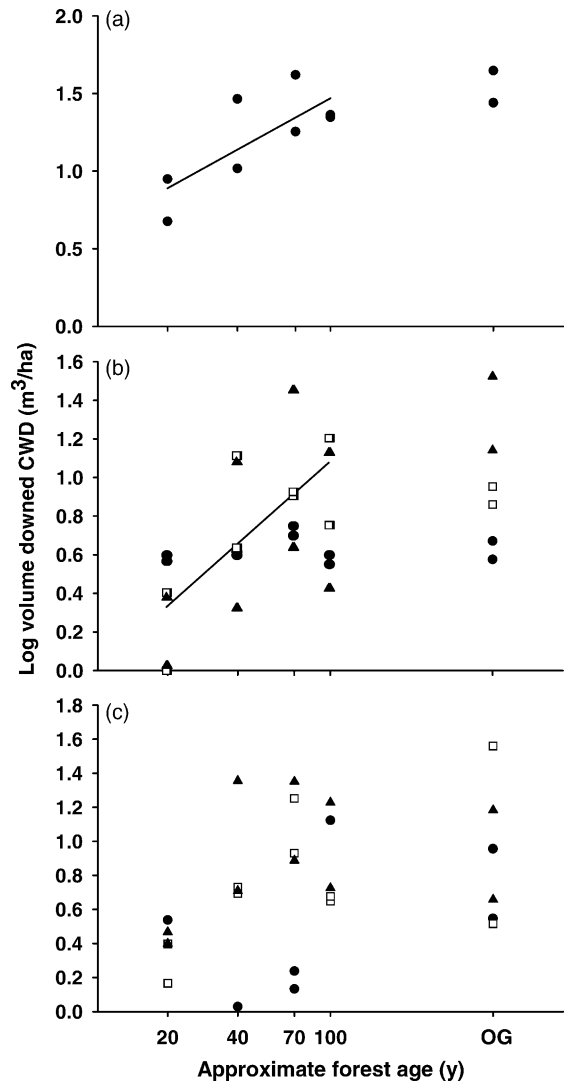


Fig. 2. Relationship between secondary forest age and (a) volume of downed CWD ($P = 0.028$, $r^2 = 0.58$), (b) volume of pieces of CWD by diameter (●, 5–10 cm; □, 10–15 cm; ▲, >15 cm; CWD 10–15 cm in diameter: $P = 0.038$, $r^2 = 0.54$), and (c) volume of pieces of CWD by decay class (●, Class 1; □, Class 2; ▲, Class 3). Only significant regressions are shown ($P < 0.05$); OG, old growth.

more than five times higher than the mean for 20-year-old stands of 6.5 m³/ha \pm 1.6 m³/ha. The relationship between DCWD volume and secondary stand age differed among the three size categories (ANCOVA: $F_{2,18} = 3.34$, $P = 0.03$). The highest volume of DCWD in young secondary forests was in small-diameter wood

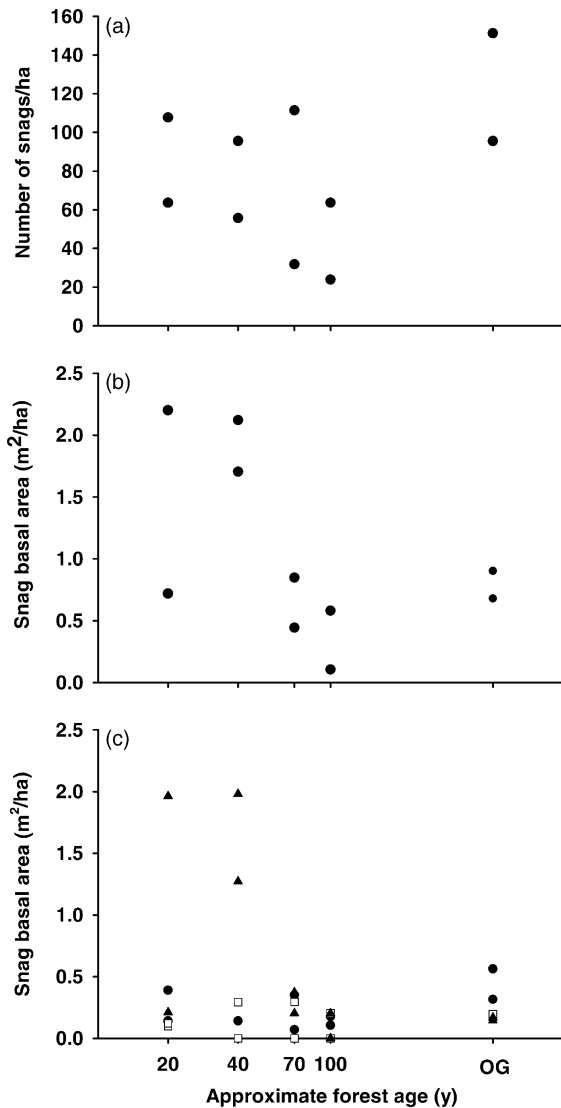


Fig. 3. Relationship between secondary forest age and (a) number of snags, (b) total snag basal area, and (c) basal area of snags with diameters 5–10 cm (●), 10–15 cm (□), or >15 cm (▲). None of the snag characteristics varied significantly with secondary forest age; OG, old growth.

(5–10 cm diameter). The volume of small and large pieces did not change significantly over secondary stand age, whereas the volume of medium diameter pieces (10–15 cm) was lower in young forest and was greater in the older secondary stands and old-growth stands (Fig. 2b). The volume of large pieces of DCWD was greatest in the old-growth forest stands. We found no

difference in the volume of DCWD of different decay levels across the chronosequence (Fig. 2c; ANCOVA: $F_{2,18} = 0.21, P = 0.81$). Most wood in the secondary forests tended to be highly decayed (Class 3).

In general, there were fewer snags in secondary than in old-growth forest, but across secondary stands, there were no significant relationship between number or basal area of snags and stand age (Fig. 3a and b). Larger snags (>15 cm diameter) were most abundant in the 20 and 40-year-old stands (Fig. 3c), but there was no pattern across stand age in the basal area represented by different sized snags (ANCOVA: $F_{2,18} = 0.85; P = 0.45$). The highest density of standing dead stems was consistently among stems in the 5–10 cm diameter class.

3.2. Vegetation composition and plant resources

Similarity of tree species composition between same-aged stands was lowest for 20-year-old stands and increased with forest age (Table 2a). The two old-growth stands were most similar of all same-aged pairs based on relative abundance of trees (60%). The similarity between secondary and old-growth stands also increased with forest age. Total species richness of trees showed little variation across secondary stand

Table 2
Average pairwise Sørensen's Similarity Indices among stands in the chronosequence based on relative abundances of (a) trees and (b) lianas

	Approximate forest age (years)				
	20	40	70	100	OG
(a) Trees					
20	15				
40	27	22			
70	24	30	26		
100	23	24	32	38	
OG	21	23	26	41	60
(b) Lianas					
20	31				
40	46	60			
70	33	44	42		
100	32	43	44	57	
OG	22	32	34	45	33

Diagonal elements are in bold and represent the similarity of two stands of the same age. Off-diagonal entries are averages of all four pairwise similarity indices of two stands of each age class; OG, old-growth forest.

Table 3

Number of tree species (*S*) in each stand and the IV of trees with small- or large-fruited bird-dispersed propagules (SF and LF, respectively); all *Ficus*, palm, and *Virola* spp.; and trees used by tent-making bats (TMB)

Approximate forest age (years) and stand replicate	<i>S</i>	Importance values					
		SF	LF	<i>Ficus</i>	Palm	<i>Virola</i>	TMB
20							
1	64	47.3	64.3	0.0	13.0	0.4	1.9
2	44	43.3	81.2	1.1	0.9	0.0	1.0
40							
1	85	51.9	63.2	2.9	14.3	0.0	1.9
2	64	67.8	42.2	3.9	18.4	1.2	2.0
70							
1	51	28.5	86.8	0.0	28.8	2.7	17.1
2	78	77.7	62.8	32.0	14.6	3.6	4.6
100							
1	74	22.6	31.8	5.0	37.2	3.9	9.1
2	63	43.1	57.6	4.4	36.3	0.0	28.1
OG							
1	74	51.8	37.6	0.0	63.8	1.2	0.0
2	75	46.9	52.3	0.9	13.7	0.0	9.2
<i>P</i>	NS	NS	NS	NS	0.005	NS	0.05
<i>r</i> ²					0.76		0.50

P-values and *r*² of significant regressions with secondary stand age are listed at the bottom of the table. NS, not significant (*P* > 0.05).

age or between secondary and old-growth forest stands (Table 3).

Similarity in liana species composition was not as predictable with forest age (Table 2b). Liana communities of the same age did not become more similar to each other with increasing forest age and the old-growth stands had a low SSI (33%). Stands of the same age were more similar to each other in their liana species composition than they were to old-growth stands. As with trees, average similarity of secondary forest liana communities to old-growth liana communities increased with stand age.

We found no difference in the total IV of species with wind versus animal-dispersed tree or liana species across the chronosequence (Fig. 4). In general, animal dispersal was more common in trees than lianas, whereas wind dispersal predominated as the dispersal syndrome for lianas. The importance of large versus small-seeded bird-dispersed species among trees did not change significantly across the chronosequence (Table 3). Large-seeded trees generally were more important than small-seeded species regardless of stand age. Fleshy-fruited species in the

understory of the BCNM included 49 understory trees, 41 shrubs, 9 herbs, and 6 understory palms. The density of understory plants producing fleshy fruits was highest in the young secondary forest and lowest in older secondary and old-growth stands (Fig. 5).

We also examined the distribution of several taxonomic groups known to be important resources for some groups of animals. *Ficus* spp. were not distributed in any predictable way across the chronosequence (Table 3), perhaps because abundances were low everywhere. We found 10 trees of *Ficus insipida*, 1 of *F. nymphaeifolia*, and 1 of *F. yoponensis*. We expected *Ficus* to be most abundant in secondary forests (Janzen, 1979; Lepš et al., 2001), but detected no such pattern. Mean IV of *Ficus* was highest in 70-year-old forest reflecting three *F. insipida* trees >130 cm dbh. However, these probably were residual trees from an earlier forest and likely are considerably older than 70 years. There was also no pattern in the importance of *Virola* spp. (*Virola sebifera* and *Virola* sp.) across the chronosequence. The importance value for all palms ≥ 5 cm dbh increased over stand age (Table 3). In part this pattern was driven by the

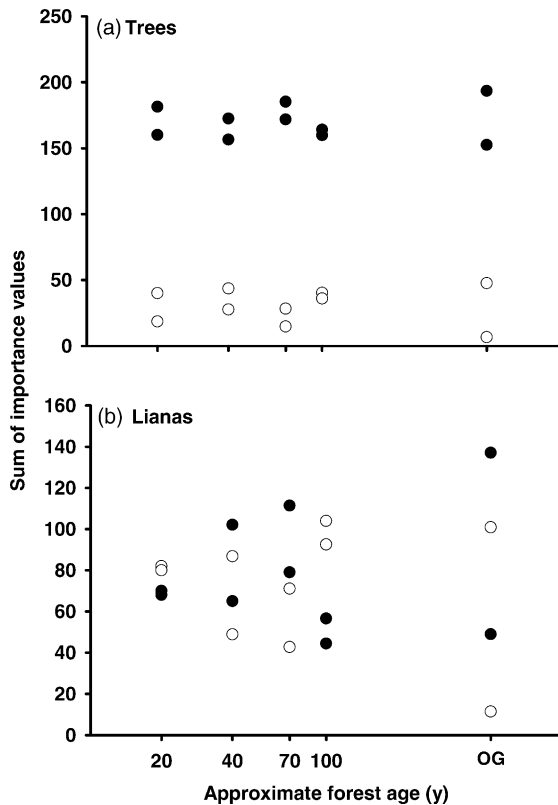


Fig. 4. Sum of importance values of species in each secondary and old-growth (OG) stand that have seeds dispersed by animals (●) or wind (○) for (a) trees and (b) lianas. The IV for trees includes all species per stand (total IV = 200), whereas the IV for lianas is only for identified liana species with the highest IV per stand totaling 150. There were no significant relationships across secondary forest age for either habit.

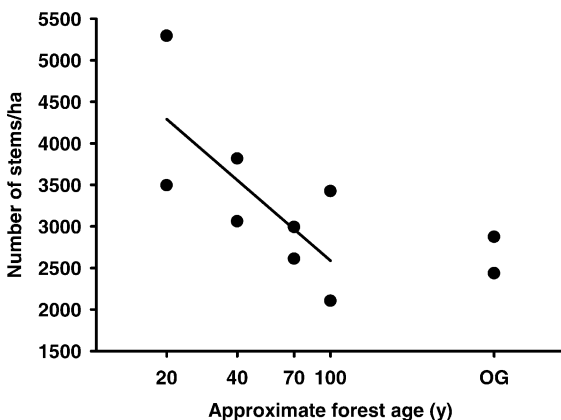


Fig. 5. Number of fleshy-fruited understory herbs, shrubs, and palms in secondary and old-growth (OG) stands ($P = 0.042$, $r^2 = 0.52$).

abundance of *Oenocarpus mapora*, which attains high importance values in old-growth stands because of its large clump sizes.

Four tree species used by tent-making bats were found on the chronosequence: *Attalea butyracea* (*Scheelea zonensis*) (Arecaceae), *Coccoloba manziniellensis* (Polygonaceae), *Astrocaryum standleyanum* (Arecaceae), and *Genipa americana* (Rubiaceae). Total importance value of these four species showed a mid-successional peak for 70 and 100-year-old stands and was low in 20 and 40-year-old stands and old growth (Table 3).

4. Discussion

4.1. Changes in forest structure

In this and other studies along the BCNM chronosequence, we found that within 70 years following cessation of active management many structural aspects of secondary forests came to resemble those of old-growth stands. Basal area (Denslow, 2000), canopy height, leaf litter mass (Denslow and Guzman, 2000), liana density (DeWalt et al., 2000), density of large living trees (≥ 65 cm dbh), snag density, volume of DCWD, and the abundance of medium-sized pieces of DCWD (10–15 cm) were all at least as great in 70-year-old secondary forest as in old growth. The BCNM chronosequence shows many similarities to that studied by Hughes et al. (1999) in the Los Tuxtlas Region of Mexico, where secondary forests were predicted to reach total above-ground biomass levels equivalent to those of old-growth forest after 73 years. In contrast, secondary forest in the Rio Negro Basin of Venezuela, where soils are less fertile, accumulates biomass more slowly and may take 190 years to achieve biomass and structure equivalent to old-growth forests (Saldarriaga et al., 1988).

Cavity-nesting birds and other animals that specialize on dead trees would find this resource to be scarce across the chronosequence, but those that use large living trees would find them to be relatively common in forests older than 70 years. In contrast, snags are both more abundant and larger in old than in young temperate forests (McComb and Muller, 1983; McGee et al., 1999). The low density of large standing dead trees in our stands may reflect the fact that

large-diameter trees in many tropical forests are more likely to snap or uproot than to die standing (Lieberman and Lieberman, 1985; Rankin-de Merona et al., 1990) or that snags are patchily distributed (Grove, 2001). For animals, the size distribution of snags may be more important than overall density; Moorman et al. (1999) suggest that snag characteristics (diameter, height, species, decay status) may be more important than total snag density in determining suitability for wildlife.

Large diameter pieces of DCWD were more common in old than in young forests. The relative scarcity of large diameter DCWD in young forests suggest that suitable dead wood may be a limiting resource for animals dependent on it. For example, cotton mice (*Peromyscus gossypinus*) use large diameter, highly decomposed stumps and fallen logs in managed pine forest in the southeastern United States (McCay, 2000). Similarly, many species of wildlife in lowland rainforests of Australia's Daintree region are dependent on large size classes of dead wood (Grove, 2001).

The low abundance of DCWD in young secondary forests also has been documented in other forest chronosequences (Saldarriaga et al., 1988; Shifley et al., 1997; Hughes et al., 1999). Significant DCWD accumulation in tropical forests is thought to occur as cohorts of early successional species senesce. In central Panama, this is thought to occur in two pulses at fallow ages of 10–30 years and again at 75–150 years (Finegan, 1996). The increases in DCWD among stands of different ages along the BCNM chronosequence were more gradual. The effect of DCWD accumulation on tropical animal populations would be an interesting avenue of research.

4.2. Changes in forest composition

Plant species composition of secondary forests did not approach that of old-growth forest as quickly as did structural aspects. Tree species richness was relatively constant over stand age, while sapling and liana richness declined with stand age (Denslow, 2000; DeWalt et al., 2000). However, species composition did differ among stand ages. On the basis of tree and liana species composition, secondary forest stands differed greatly among themselves and with old-growth stands. Although similarity to old-growth composition increased with secondary forest age,

100-year-old secondary stands and old-growth forests still had only a Sørensen's Similarity Index of 41% for trees and 45% for lianas. Thus, our data suggest that secondary forest species composition converges on old-growth forests more slowly than does forest structure, as previously noted by Guariguata and Ostertag (2001).

Despite such floristic differences, food resources for generalist frugivores were common throughout the chronosequence, and in some instances more common in secondary than in old-growth forests. Early successional plants tend to have small dehiscent fruits (Opler et al., 1980), but by 20 years animals were the predominant seed vector for trees across the chronosequence. More lianas than trees were wind dispersed, but there was no indication that forest of any age was more depauperate in fleshy-fruited lianas. Secondary forest may be better habitat for small generalist frugivores than old-growth forest because the density of fleshy-fruited plants in the understory was greater in young than old stands. Similarly, large frugivorous birds may find abundant fruit of all sizes across the chronosequence. In addition, our data do not suggest that *Ficus* or *Virola* species are any more abundant in old than in young forests. Individuals of both genera were patchily distributed. However, this and other studies found palms to be scarce in young secondary forests but abundant in old growth (Guariguata et al., 1997; Farris-Lopez, 2001). Palms are an important source of food for many taxa during periods of overall food scarcity on Barro Colorado Island (Foster and Brokaw, 1982; DeSteven et al., 1987; Peres, 1994); low palm abundance in young secondary forests suggests that they would not be as good a source of food during famines as old-growth forest.

In the BCNM chronosequence, trees used by the tent-making bat, *U. bilobatum* were scarce in early secondary forest. However, large-leaved herbs also used for tents, such as *Heliconia* (Musaceae) and *Calathea* (Marantaceae) spp., generally are abundant in early second growth (Denslow, unpublished data), suggesting that nesting sites for this species may be available even in young stands.

4.3. Conservation of secondary forests

Our data describe patterns of forest succession following large-scale clearing and long-term use of

land in a tropical moist forest environment of central Panama. We suspect that the study areas are representative of reforested landscapes following habitat fragmentation produced by agriculture, ranching or clear-cut logging, in which small patches of old forest remain in a matrix of cleared, managed or fallow farmland (Laurance et al., 1998; Read et al., 2001). Patterns and rates of succession will reflect land-use history, the proximity of remnant patches of old growth, and soil characteristics. For example, rates and patterns of secondary succession on nutrient poor soils of the Rio Negro Basin of Venezuela differ from the patterns on the richer soils of central Panama (Saldarriaga et al., 1988; Fearnside and Guimarães, 1996; Denslow, 2000). The patterns we observed likely are not representative of once-forested land where inadequate seed sources or dispersal agents remain and where short clearing and regrowth cycles result in depauperate, low-stature vegetation. Nor are they representative of highly disturbed old forest in which selective removal of timber or minor forest products alter forest structure and composition. The patterns we have described are expected to occur during an uninterrupted successional process. Similarly, distribution and availability of resources and suitable habitat in the landscape are important for colonization and maintenance of wildlife populations.

Our results and those of others suggest that secondary forests as young as 20 years old may provide a good resource base for some species, in particular birds and mammals with mixed diets of insects and fruits. Previous studies of bird diversity and abundance from a variety of forests have found that use of secondary forest by birds approaches that of old-growth around 25 years after land abandonment (Bowman et al., 1990; Raman et al., 1998). Moreover, secondary vegetation may be critical habitat for some birds (Karr, 1990; Loiselle and Blake, 1994). Two-thirds of the species losses that occurred on BCI following the filling of Lake Gatun between 1910 and 1914 took place as early second growth developed into forest (Willis, 1974; Willis and Eisenmann, 1979). In contrast, species dependent on structural attributes of old-growth forests, such as cavity nesters and those dependent on coarse-woody debris, may find adequate foraging or nesting sites only in forests at least 70 years old. Species dependent on large snags may be limited throughout the chronosequence.

Overall, secondary succession from pasture and agriculture proceeded rapidly with some ecosystem and structural characteristics converging on old-growth forest patterns within 20 years of regrowth. On the other hand, young secondary stands (20 and 40 years) in this study still lacked some structural characteristics indicative of older forests in central Panama (e.g. DCWD volume and large trees) and floristic differences were still present even after 100 years following abandonment. How critical these differences are for specific taxa can only be examined with direct study of wildlife populations across the chronosequence. Nonetheless, forest restoration by natural or directed successions may provide valuable wildlife habitat for generalist species and the management and distribution of secondary forests should be an important component of any large-scale conservation strategy in the tropics. However, old-growth tropical forests are becoming scarce and fragmented in many landscapes and they are being replaced, not by secondary forests, but by pasture, early fallow vegetation, and permanent agriculture (e.g. Read et al., 2001). If secondary forests are to play a role in the conservation of tropical plants and animals, we will need to protect them too from exploitation and disturbance.

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