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ECOLOGICAL PROPERTIES FOR THE EVALUATION, MANAGEMENT, AND RESTORATION OF TEMPERATE DECIDUOUS FOREST ECOSYSTEMS[1]

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Abstract. Given that many of the original deciduous forests of North America have disappeared over the last few centuries, our challenge is to preserve remnant forests, restore altered forests, and harvest managed forests in a sustainable manner. To do so, we need to identify macroscale properties that can easily monitor the condition of the eastern deciduous forest as a whole. We offer 10 possible properties: (1) tree size; (2) canopy composition; (3) quantity and quality of coarse woody debris; (4) number of spring ephemeral species in the herbaceous layer; (5) number of typical corticulous bryophyte species; (6) density of wildlife trees; (7) fungi; (8) avian community; (9) number of large carnivores; and (10) forest area. We have assigned to each property a control (or normal) value, an intermediate value, and a heavily altered value. These values are based on the existing literature.

These 10 properties would: (1) allow us to recognize, rank, and protect high-priority forest sites for conservation; (2) tell us whether changes in a forest are in the direction of restoration or toward further alteration; and (3) enable us to evaluate different harvesting methods so we can select those that cause the least alteration to forests.

Key words: avian community; carnivores; canopy composition; coarse woody debris; corticulous bryophytes; ecological properties; ecosystem integrity; evaluation; forest area; fungi; herbaceous layer; management; restoration; temperate deciduous forest; tree size; wildlife trees.

INTRODUCTION

Only a few generations ago, eastern North America was covered by deciduous forest (Fig. 1). Similar forests covered western Europe and eastern Asia. They were remnants of the great Arcto-Tertiary forests that once covered much of the Northern Hemisphere (Braun 1950, Daubenmire 1978, Rohrig 1991). Today those great forests are largely gone (Bormann and Likens 1979, Dunn et al. 1991, Riley and Mohr 1993). We could guarantee an adequate wood supply for future generations, and solve many conservation problems, through four steps: (1) managing remaining forest areas sustainably; (2) restoring altered forests to their original composition; (3) replanting areas from which forest cover is absent; and (4) protecting ecological reserves and parks to represent remnants of this original forest and to provide baselines for scientific research.

If we take such a visionary approach, we can restore our forests and our forested landscape to one where a wide range of forest-related activities can coexist (Fig. 2).

In order to achieve these four steps, we need to study the properties of temperate deciduous forests. Our first inclination may be to assume that questions about the properties of forests deal primarily with tree species composition. We may think of forests merely as a list of dominant tree species. Tree composition is one property—comparable to the hair color of a human being. But there are many other properties we can try to describe. Consider: what were the original food webs like? How many bird species typically nest or feed in the canopy? How much detritus is found on the forest floor? How many kinds of insect species feed on the trees? What is the rate of nitrogen fixation in forest soils? What are rates of decomposition of fallen trees? Which animal species disperse which species of tree seeds?

Our challenge is to find properties that allow us to measure these many different aspects of the ecology of deciduous forests. Choosing properties is difficult because we still lack quantitative scientific models of forests that tell us which properties are most important in maintaining function, sustaining productivity, and predicting future behavior. For example, we know that mass and velocity are important for physical systems, but what are the equivalents in ecology? To look for properties, we can turn in three directions. (1) There is the growing literature on the health and integrity of ecosystems (e.g., Rapport et al. 1985, Schaeffer et al. 1988, Karr 1991, Woodley et al. 1993). Here we may find some suggestions for the kinds of properties that need measuring. (2) We can use our intuition and field experience as to the kinds of properties that seem to vary among forest stands. (3) We can return to the original forests that once covered this landscape. We know that these forests persisted for thousands of years, and, on larger scale, survived no less than four ice ages.

If we use the analogy of ecosystem health or integrity, then we argue that certain characteristics, such as the presence of large organisms or high diversity, are desirable properties that indicate higher levels of health

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FIG. 1. The Eastern Deciduous Forest region of North America (from Braun 1950).

or integrity. Intuition and experience guide us to more qualitative measures, such as the presence of rare species of warblers, orchids, or other desirable organisms. Or, returning to the remnants of the original forest, we can ask which essential properties of temperate deciduous forests (1) are easy to measure and monitor and (2) compare macro- rather than microscale properties (Keddy 1991). These might include tree size, canopy composition, the presence of large carnivores, the diversity of spring ephemerals, and the amounts of coarse woody debris. We have used this third approach. We use the existing literature to estimate values for these state variables in forests with little human alteration, and then present values that indicate moderate or high levels of modification for each. This method is an avowedly pragmatic approach (sensu James 1907). We looked for state variables that were easy to measure, had existing data, and seemed to measure a wide variety of functions. This approach complements the international move to develop criteria and indicators for the conservation of temperate and boreal forests (Canadian Forest Service 1995). As new information becomes available, the list of properties can be modified and extended.

The properties identified could represent a continuum of ecological scales. At one end is the stand scale; at the other end is the landscape scale. We have placed the emphasis upon stand characteristics for several reasons. (1) Most often it will be stands that we wish to evaluate in the field. (2) Computer models often are based upon stands. (3) The stand scale is the least understood, and by choosing it, we have started with the biggest problem first. We already know that area and connection are the two most important characteristics at the landscape scale (Poser et al. 1993, Riley and Mohr 1993), and additional landscape properties can be added relatively easily in future years. (4) Careful selection of stand characteristics will integrate the landscape scale quite naturally. One reason for using large carnivores in our list of properties, for example, is that they range over large distances, and so integrate landscape characteristics. They may measure landscape properties better than we can.

It is not enough to list essential properties. We must also determine, or at least estimate, a control or reference value for each. We have done this by collecting reported values of these properties from published and unpublished studies on tracts of forest with minimal human alteration. Such a course could lead to difficult semantic problems as we debate how to define and recognize virgin, pristine, primary, undisturbed, presettlement, old-growth, natural, healthy, or integrated forest types. This area is fraught with problems (Botkin 1990, Nowacki and Trianosky 1993). There are the semantic difficulties as to what we mean by "natural" or "virgin" forest—Pre-European? Pre-ice age? Pre-aboriginal? There are also methodological problems: even if we agree upon an era to use for reference, how do we determine what the properties of such forests actually were? We avoid such debates. We are conducting an empirical exercise, not a philosophical one. We simply examine forests in eastern North America that have had little human alteration, and describe their

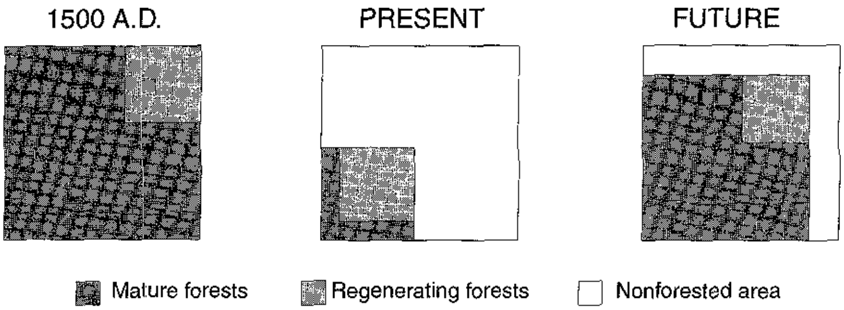

FIG. 2. A past, present, and suggested future condition of the Eastern Deciduous Forest.

TABLE 1. Basal area of primary forest stands.

Basal area (m^2/ha)*	Study site†	Forest type	Source
Old-growth stands			
28	Michigan	*Fagus–Acer*	Schmelz and Lindsey (1965)
32	Pennsylvania	*Tsuga–Fagus*	Hough (1936)
40	Ohio	*Acer–Fagus*	Boerner and Cho (1987)
29	Indiana	*Fagus–Acer–Quercus*	Lindsey et al. (1958)
28	Indiana	*Acer–Fagus*	Abrell and Jackson (1977)
26	Indiana	*Fagus–Acer*	Schmelz and Lindsey (1965)
26	Indiana	*Acer*	Schmelz and Lindsey (1965)
23	Indiana	*Fagus–Acer*	Schmelz and Lindsey (1965)
32	Ohio	*Acer–Quercus*	McCarthy et al. (1987)
30	Kentucky	Deciduous	Bougher and Winstead (1974)
($\bar{X}$ = 29, SD = 4)			
Altered sites			
24	New Hampshire	*Fagus–Acer–Betula*	Whittaker et al. (1974) Logged 57 yr before study
21	Tennessee	*Acer saccharum*	Onega and Eickmeier (1991) Nonclimax site
19	Indiana	Upland deciduous	Schmelz and Lindsey (1965) Recently altered forest
($\bar{X}$ = 21, SD = 3)			

* Altered sites' basal areas based on a minimum stem diameter of 10.2 cm, except Boerner and Cho (1987) and McCarthy et al. (1987) used 2.5 cm and Hough (1936) used 9.1 cm. Values have been rounded up to the even number.

† *Study sites are listed in the order of ascending latitude.*

properties. We assume, optimistically, that by proceeding in this simple descriptive manner there will be broad agreement among scientists and managers regarding the coarse-scale properties of pre-European forests. The data can speak for themselves.

LIST OF PROPERTIES

1) *Tree size.*—Tree size has been defined in terms of basal area per hectare, since this was found to be the most commonly used measurement in the literature. The mean basal area of 10 primary forest sites was 29 m^2/ha (SD = 4) (Table 1). For those who think in terms of mean diameter at breast height (dbh), this basal area roughly corresponds to trees with a 40–50 cm dbh. The 10 basal area measurements for the primary forests were very similar, and therefore might be considered a property of temperate forests. Held and Winstead (1975) came to the same conclusion after comparing the basal areas of seven different mesic primary forest systems, which they found to approximate 30 m^2/ha. Three of their studies are used here. Similarily, Woods and Cogbill (1994) cite basal areas of 23–63 m^2/ha in the Adirondack Mountains of New York, the highest values being found in hemlock stands.

Reductions in basal area do not necessarily indicate human alteration; they could be due to variations in soil moisture, stand aspect, latitude, and species composition. Based upon the above figures, we propose three preliminary categories: control/normal (>29 m^2/ha), intermediate (20–29 m^2/ha), and low (<20 m^2/ha).

2) *Canopy composition.*—The canopy of mature deciduous forests is usually dominated by only a few species, while young forests tend to incorporate a larger number of tree types (Doyle 1980, Wang and Nyland 1993). This general rule is, of course, dependent on the latitude since species diversity tends to increase southward. This property is shown in Table 2; three species or less constitute the majority of canopy trees in the eight old-growth forests cited.

Tree species in deciduous forest can be arranged along a continuum from shade tolerant to shade intolerant (Spurr and Barnes 1980). The proportion of intolerant species increases with the intensity of disturbance, with areas of second-growth forest or abandoned agricultural land often being dominated by intolerant species. Prior to human settlement, such shade-intolerant species probably comprised only ≈2–10% of the relative density of trees, and ≈2–16% of the relative basal area of the forest (Wang and Nyland 1993). Their presence was maintained through natural processes of windthrow gap creation, fire, and hurricanes (e.g., Runkle 1985, Foster 1988, Barnes 1991). Human-induced activities have greatly increased their abundance and distribution. Following clear-cutting, shade-intolerant species may comprise up to one-half of the long-lived trees in the upper canopies of forest stands (Wang and Nyland 1993).

The proportion of tolerant species can therefore be used as a property. The tolerant species used might vary with geographic region, but simply using the proportion of American beech, sugar maple, basswood, and hemlock trees >10 cm dbh will provide a comparison at the coarse scale. We propose three categories: control/normal (>70%), intermediate (30–70%), and heavily altered (<30%).

3) *Coarse woody debris.*—Coarse woody debris (CWD) generally includes fallen logs, snags, and large branches. CWD provides a necessary microhabitat for

TABLE 2. The relative densities of canopy species in eight unaltered forest sites.*

Species	Study site†,‡ 1	2	3	4	5	6	7	8
Fagus grandifolia	17	19	15	22	58	53	74	
Acer saccharum	13	14	12	34	5	33	8	69
Tsuga canadensis	7	20	41		20	1		
Halesia carolina	30	20	23					
Aesculus octandra	3	8	1	20				
Quercus alba						+		
Tilia americana								20
Acer rubrum	1				7	6	6	+
Quercus borealis							4	2
Ulmus americana						1	6	6
Prunus serotina							4	
Tilia heterophylla	8	7		11		+		+
Liriodendron tulipifera	9		1			3		+
Carya ovata						1		
Nyssa sylvatica								
Carya glabra	2							
Quercus rubra	1					+		
Fraxinus americana	4	2		4		1		+
Magnolia fraseri	1	1						
Magnolia acuminata	2					+		
Betula lutea + *B. lenta*	3	6	1		6			
Platanus occidentalis								
Sassafras varriifolium						+		
Castanea dentata						1		
Ostrya virginiana						1		
Carpinus caroliniana						+		
Other		3	6	9	4			
No. species constituting 70% of the relative density	5	4	3	3	2	2	1	2
No. species having >15% relative density	2	3	3	3	2	2	1	2

* Except for Site 7 (some selective cutting of *Quercus* and *Tilia* 65 yr before study) and Site 8 (some stands may have once been selectively cut). Sites exclude oak forests of Piedmont areas and conifer-dominated stands.

† Relative stem density per hectare, except for Stand 8, which is the Mean Relative Density for nine stands. Values have been rounded up to the even number. The symbol + is used for a relative density <0.5.

‡ Study site locations and sources (listed in order of ascending latitude): 1. North Carolina (Lorimer 1980); 2. South Appalachians (Runkle 1981); 3. South Appalachians (Runkle 1981); 4. North Carolina (Runkle 1981); 5. Pennsylvania (Runkle 1981); 6. Ohio (Williams 1936); 7. Michigan (Cain 1935); 8. Minnesota (Rogers 1981).

many forest organisms including birds, mammals, herptiles, invertebrate decomposers, bryophytes, fungi, and tree seedlings. The amount of CWD in a forest is affected by its disturbance history and successional stage (Harmon et al. 1986). CWD values increase with stand age, being lowest in 40–57-yr-old stands, and highest in very old forest areas (unpublished data [Tritton 1980] reviewed by Harmon et al. 1986). A young stand (i.e., 20 yr) may have high CWD levels, which can be attributed to remnant woody material left from a great disturbance, i.e., slash left after logging, or snags and logs left after fire, disease epidemics, etc.

CWD values for tracts of eastern deciduous forest vary with latitude, warmer and moister southern climes having greater decomposition rates and lower CWD accumulation (MacMillan 1981). Another source of variation arises from differences in methodology (Harmon et al. 1986), such as what diameter of wood is measured, and whether the CWD includes logs, snags, and large branches. Despite these problems, there is some similarity in published values (Table 3). Bormann and Likens (1979) had comparable values, finding 28–34 Mg/ha in 170-yr-old northern hardwoods in New Hampshire. Tritton's data has a considerably higher CWD value of 49.3 Mg/ha for a 200-yr-old *Acer–Fagus* stand (Harmon et al. 1986). However, the CWD values for his 30- and 60-yr-old *Acer–Fagus* stand are half that of his old-growth forest. Bormann and Likens (1979) suggest that the low estimates for woody biomass in clear-cut northern hardwood forests may be due to an initial rapid decrease in CWD density, which is probably due to the digestion of readily metabolized compounds, such as hemicellulose and cellulose (MacMillan 1981). Table 3 has CWD values for old-growth forests that are, with one exception, >20 Mg/ha. Based upon these figures, we propose three categories: control/normal (>20 Mg/ha), intermediate (10–20 Mg/ha), and low (<10 Mg/ha). These values are obviously difficult to estimate in the field.

A simpler indicator would take into consideration the wood's size and state of decay. Primary forests would have had large, heavily decayed logs. That is to say, the logs would have been >40 cm dbh, and had a decay class of 5 (no bark, twigs, or branches re-

TABLE 3. Amount of coarse woody debris (CWD) in old-growth forests.

CWD (Mg/ha)	Minimum stem size (cm)*	Wood type†	Site	Forest type	Source‡
Old growth					
49	3.0	ls	unknown	*Acer–Fagus*	1
17	5.0	lf	Indiana	*Quercus* mixed	2
22	20.0	lsf	Kentucky	*Quercus–Fagus*	3
29	7.5	l	unknown	*Fagus–Betula*	4
24	7.5	l	unknown	*Quercus* mixed	4
21	7.5	l	unknown	*Quercus primus*	4
($\bar{X}$ = 27, SD = 11)					
Altered sites					
14	3.0	ls	Tennessee	Nonclimax	5
21	3.0	ls	unknown	30 yr *Acer–Fagus*	4
23	3.0	ls	unknown	60 yr *Acer–Fagus*	4
($\bar{X}$ = 19, SD = 5)					

* Values rounded up to the even number.

† l—logs, s—snags, and f—fragments.

‡ Sources: 1. Tritton, *unpublished data*, cited in Harmon et al. (1986); 2. MacMillan (1981); 3. Muller and Liu (1991); 4. Harmon, *unpublished data*, cited in Harmon et al. (1986); 5. Onega and Eickmeier (1991).

maining; at least 50% bryophyte cover; oval in cross section) (MacMillan 1981). MacMillan (1981) found a fairly consistent input of large-diameter logs (>40 cm dbh) over his 23-yr study in an Indiana old-growth forest. Similarly, a primary forest would have large CWD with varying ages and levels of decomposition. Based on MacMillan's data, Table 4 suggests three categories for CWD in forests: control/normal (both firm and crumbling large logs present), intermediate (either firm *or* crumbling large logs present), and low (large logs absent). The term "firm" includes logs that are soft enough to be broken apart with a hammer; "crumbling" logs have little structural integrity.

4) *Herbaceous layer.*—One property of temperate deciduous forests is a diverse spring flora. Since floras vary greatly with latitude and site conditions, it is necessary to select a characteristic subset to use as a property. Givnish (1987) identified seven guilds of forest herbs based on the timing of their leaf production. One could select a set of indicator species by choosing one or more of these guilds. Alternatively, one could examine species lists from different sites in order to compile a list of "typical" forest species. In either case, not every woodlot would have all the species listed simply due to regional variability in distribution. Therefore, a site would not be considered deficient because the herb assemblage was missing certain species. We will combine both approaches. Table 5 lists spring ephemerals (sensu Givnish 1987). The list also includes species that Givnish considered early summer herbs. In any case, all these species emerge and photosynthesize primarily before tree leaf expansion.

TABLE 4. The presence of large decaying logs in forests of varying disturbance levels. Presence is defined as ≥8 logs/ha. Large logs have at least a 40 cm dbh.

Disturbance level	Firm large logs	Crumbling large logs
Undisturbed or primary	+*	+
Intermediate	+	−
Disturbed	−	+
Heavily altered	−	−

* + present, − absent.

Forest herbs may actually benefit from small canopy gaps created by windthrow (Collins et al. 1985). Thus, the herbaceous layer may be relatively insensitive to selective logging. Reader (1987) found that few common herbs were lost from mature forest stands following selective cutting, and that the percentage of herbaceous species lost did not increase significantly with an increase in cutting intensity. Similarly, Metzger and Schultz (1984) looked at the long-term effects of logging, and found that clear-cut and selectively cut stands had similar herb composition after 50 yr, both having returned to what was typical of hardwood forests.

Forest herbs are, however, sensitive to grazing and in heavily grazed woodlots only two of the listed species appear to survive—*Claytonia virginica* and *Erythronium americanum* (P. Keddy, *personal observation*). Forest herbs have limited seed dispersal, being primarily ant dispersed (Thompson 1980). Species like *Erythronium americanum* propagate by vegetative means, which also makes for slow colonization rates (Struik and Curtis 1962). Some species such as *Caulophyllum thalictroides* and *Podophyllum peltatum* produce fruit for mammalian seed dispersers, but even so appear to be slow to recover from grazing. Table 5 suggests three categories: control/normal (≥6 species), intermediate (2–5 species), and low (<2 species).

5) *Corticulous bryophytes.*—Forest type, tree species, tree size, bark roughness, bark pH, and moisture may all control the distribution of corticulous cryptogams (i.e., mosses, liverworts, and lichens). Hale (1955) compared the corticulous cryptogam communities of forest stands that varied in their stage of suc-

TABLE 5. Spring ephemerals of mature deciduous forest.

Species†	Study‡						
	1	2	3	4	5	6	7
Tiarella cordifolia	*	*	*		*		
Dentaria diphylla	*	*	*		*		
Podophyllum peltatum	*	*		*	*	*	
Polygonatum biflorum	*	*	*	*	*	*	
Caulophyllum thalictroides	*	*	*		*		*
Trillium grandiflorum	*		*	*	*		*
Claytonia virginica	*	*		*	*	*	*
Erythronium americanum	*				*		*
Dentaria laciniata	*			*		*	*
Sanguinaria canadensis	*			*		*	
Dicentra cucullaria				*	*	*	
Allium tricoccum				*	*	*	
Maianthemum canadense			*				*
Dicentra canadensis				*	*	*	*
Total number of species	10	6	6	9	11	8	7

† Nomenclature follows Gleason and Cronquist (1963).

‡ Study site locations, forest types, and sources (listed in the order of ascending latitude): 1. Kentucky, *Fagus–Acer* (Braun 1942); 2. Appalachians, mixed hardwood (Cain 1943); 3. Pennsylvania, *Acer–Fagus* (Hough 1936); 4. N. Ohio, *Acer–Fagus* (Vankat and Snyder 1991); 5. Ohio, *Acer–Fagus* (Williams 1936); 6. S. Ohio, *Fagus–Acer* (Moore and Vankat 1986); 7. Michigan, *Acer–Fagus* (Brewer 1980).

cession. Using the continuum index developed by Curtis and McIntosh (1951), Hale found that corticulous cryptogams were related to the forest environment, with light intensity being a significant environmental factor. Patterson (1940) came to the same conclusion as Hale, but included evaporational tension as an influential environmental factor. Billings and Drew (1938) described bryophyte associations on various deciduous trees, including *Fagus grandifolia,* and related them to the characteristics of the bark. Phillips (1951) concluded that bark-inhabiting bryophytes were dependent on moisture levels of the bark. Some epiphytes, such as *Pulmonaria* lichens, are known to fix atmospheric nitrogen, thereby increasing soil fertility. In the field experience of the authors, stands of young second-growth forest have a poorly developed bryophyte flora.

TABLE 6. Corticulous bryophytes found on deciduous forest trees.†

Species‡	Study§						
	1	2	3	4	5	6	7
Anomodon rugelii	*	*	*	*			
Brachythecium oxycladon	*	*	*	*			
Neckera pennata	*	*		*		*	*
Anomodon attenuatus	*		*	*		*	*
Radula complanata	*			*		*	*
Frullania eboracensis		*			*	*	*
Porella platyphylla (incl. *Porella latyphylloidea*)		*		*		*	*
Schwetschkeopsis denticulata	*	*	*				
Anomodon triste		*	*	*			
Cololejeunea biddlecomiae		*	*	*			
Orthotrichum pumilum		*			*		*
Homomallium adnatum		*				*	*
Ulota crispa		*		*			*
Anomodon minor					*	*	*
Dicranum fulvum		*		*			
Leucodon brachypus		*		*			
Metzgeria furcata		*		*			
Radula caloosiensis		*	*				
Amblystegium varium				*	*		
Platygerium repens				*	*		
Mnium cuspidatum					*	*	
Haplohymenium triste						*	*

† Tree species considered are *Fagus grandifolia, Acer saccharum,* or *Acer rubrum.*

‡ The list contains only those species cited in two studies or more.

§ Study site locations, species studied, and sources (listed in order of ascending latitude): 1. E. Tennessee, *Fagus grandifolia* (Billings and Drew 1938); 2. Tennessee, *Fagus grandifolia* (Cain and Sharp 1938); 3. Tennessee, *Acer saccharum* (Cain and Sharp 1938); 4. Virginia, *Fagus grandifolia, Acer saccharum, Acer rubrum* (Patterson 1940); 5. Southern Wisconsin, *Acer saccharum* (Hale 1955); 6. Northern Wisconsin, hardwood species (Hale 1952); 7. Michigan, *Acer saccharum, Fagus grandifolia* (Phillips 1951).

TABLE 7. Cavity-dwelling birds and mammals of the Eastern Deciduous Forest (after Tubbs et al. 1987 and Harmon et al. 1986).

		Use				
Species	Excavator	Perch	Forage	Nest	Roost	Den
Wood Duck *(Aix sponsa)*	secondary			*		
Common Goldeneye *(Bucephala clangula)*	secondary			*		
Hooded Merganser *(Lophodytes cucullatus)*	secondary			*		
Common Merganser *(Mergus merganser)*	secondary			*		
Turkey Vulture *(Cathartes aura)*	secondary	*		*		
Barred Owl *(Strix varia)*	secondary	*		*		
Eastern Screech Owl *(Otus asio)*	secondary	*		*	*	
Northern Saw-whet Owl *(Aegolius acadicus)*	secondary	*		*	*	
Common Flicker *(Colaptes auratus)*	primary	*	*	*	*	
Pileated Woodpecker *(Dryocopus pileatus)*	primary	*	*	*	*	
Red-bellied Woodpecker *(Centurus carolinus)*	primary	*	*	*	*	
Red-headed Woodpecker *(Melanerpes erythrocephalus)*	primary	*	*	*	*	
Yellow-bellied Sapsucker *(Sphyrapicus varius)*	primary	*	*	*	*	
Hairy Woodpecker *(Dendrocopus villosus)*	primary	*	*	*	*	
Downy Woodpecker *(Dendrocopus pubescens)*	primary	*	*	*	*	
Great Crested Flycatcher *(Myiarchus crinitus)*	secondary			*		
Black-capped Chickadee *(Parus atricapillus)*	primary			*	*	
Carolina Chickadee *(Parus carolinensis)*	primary			*	*	
Tufted Titmouse *(Parus bicolor)*	secondary			*	*	
Red-breasted Nuthatch *(Sitta canadensis)*	secondary		*	*	*	
White-breasted Nuthatch *(Sitta carolinensis)*	secondary		*	*	*	
Brown Creeper *(Certhia familiaris)*	secondary		*	*	*	
House Wren *(Troglodytes aedon)*	secondary		*	*	*	
Winter Wren *(Troglodytes troglodytes)*	secondary		*			
Bewick's Wren *(Thryomanes bewickii)*	secondary		*			
Carolina Wren *(Thryomanes ludovicianus)*	secondary		*			
Eastern Bluebird *(Sialia sialia)*	secondary	*	*	*		
Tree Swallow *(Iridoprocne bicolor)*	secondary		*	*		
Big brown bat *(Eptesicus fuscus)*	secondary			*		
Little brown bat *(Myotis lucifugus)*	secondary			*		
Indiana myotis *(Myotis sodalis)*	secondary			*		
Silver-haired bat *(Lasionycteris noctivagans)*	secondary			*		
Southern red-backed vole *(Clethrionomys gapperi)*	secondary				*	
Deer mouse *(Peromyscus maniculatus)*	secondary				*	

TABLE 7. Continued.

Species	Excavator	Use				
		Perch	Forage	Nest	Roost	Den
Southern flying squirrel (*Glaucomys volans*)	secondary					*
Northern flying squirrel (*Glaucomys sabrinus*)	secondary					*
Grey squirrel (*Sciurus carolinensis*)	secondary					*
Red squirrel (*Tamiasciurus hudsonicus*)	secondary					*
Porcupine (*Erethizon dorsatum*)	secondary					*
Grey Fox (*Urocyon cinereoargenteus*)	secondary					*
Black bear (*Ursus americanus*)	secondary					*
Raccoon (*Procyon lotor*)	secondary					*
Marten (*Martes americana*)	secondary					*
Fisher (*Martes pennanti*)	secondary					*
Ermine (*Mustela erminea*)	secondary					*
Long-tailed weasel (*Mustela frenata*)	secondary					*

This may be the result of existing trees being too young to support epiphytes and there being no large old trees as a source of colonization.

After comparing these and other studies, a list was made of the corticulous bryophyte species expected to be found in mesic old growth beech-maple forests (Table 6). Based on Table 6, we propose three categories: control/normal (≥7 species), intermediate (2–6 species), and low (<2 species).

6) *Wildlife trees.*—At least 28 birds and 18 mammals of the Eastern Deciduous Forest require wildlife trees for a variety of functions—perching, foraging, nesting, roosting, and denning (Table 7) (Harmon et al. 1986, Tubbs et al. 1987). There are two general groups of studies on wildlife trees. Some measure the number of "snags" (dead trees that are still standing), and some measure the number of "cavity trees" (excavated live trees having broken tops and limbs, and suffering from central decay). It is difficult to compare the results of the studies since each study uses different parameters, such as forest type and disturbance history. However, some papers agree on general snag characteristics of old forests. Old-growth stands seem to have lower densities of snags than younger forests. MacDonald (1992) found that snag densities ranged from 16.3 to 97.3 snags/ha, with primary stands having the lowest densities. Carey (1983) also found that old-growth forests (*Acer–Fagus–Betula* composition) had the lowest snag densities in a comparison of forests ranging from 22.4 to 55.1 snags/ha. McComb and Muller (1983), while their snag density measurements were an order of magnitude larger than the last two studies, also found old-growth stands had much lower snag densities per hectare than second-growth stands (312.3 vs. 741.2, respectively). Furthermore, it has been found that primary forests have proportionally more large-diameter snags (>50 cm dbh) than any other forest type (Spies et al. 1988, MacDonald 1992), and it is large-diameter snags that support the greatest number of snag-dependent species.

TABLE 8. Estimates of large-diameter cavity/den tree densities required to provide cavity/den sites for viable populations of cavity-dwelling wildlife species (from Tubbs et al. 1987).

Geographical location	Minimum stem size dbh (cm)	No. stem density (no./10 ha)
Northeast	>46	0.88
Northeast	>46	0.96
Missouri	>48	4.00

The existing data show that wildlife trees are essential components of a forest. What is not clear is the number and size of trees expected. Table 8 offers us a minimum number of cavity trees that a forest needs to support healthy populations of wildlife. As a first approximation, we used MacDonald's data (Table 9) to estimate the number of cavity trees >50.8 cm dbh present in old-growth forests. Based on this data, we propose three categories: control/normal (≥4 wildlife trees/10 ha), intermediate (1–3 wildlife trees/10 ha), and low (<1 wildlife tree/10 ha).

7) *Fungi: macrofungi.*—A final stand property would measure fungi. We have not incorporated it into the evaluation system because of insufficient availability of data. It is a high priority for future work. Little is

TABLE 9. Presence of large-diameter snags of old-growth forests in Ontario (from C. MacDonald, *personal communication*).

Stand area (ha)	Number of snags present		Snag density (no./10 ha)	
	38.1–50.7 cm dbh	>50.8 cm dbh	>38.1 cm dbh	>50.8 cm dbh
11	1	5	5.5	4.5
47	3	7	2.1	1.5
21	4	0	1.9	0
8	1	2	3.8	2.5
12	11	10	17.5	8.3

known about the relationship between the macrofungal community and its habitat (Hawksworth 1990). European scientists have only recently begun gathering macrofungi data into "red data lists," while North American research has not even reached that stage. Macrofungi diversity is difficult to enumerate since the hyphae are difficult to find and identify, and fruiting bodies may not appear seasonally or even yearly, making long-term studies necessary. More mycological research is needed before measurable values can be determined; nevertheless, we believe that the macrofungi are a promising characteristic of primary forests that deserves more work.

Mycologists studying old-growth deciduous forests have found a great number of wood-decaying macrofungi that are not seen elsewhere (S. Redhead, *personal communication*). In addition, late-successional tree species in many forest types around the world depend on mycorrhizae [ectomycorrhizal (EM)- and endomycorrhizal (VAM)-forming fungi] for regeneration and perpetuation (Perry et al. 1988). These fungi offer their host trees protection from drought, cold and disease, and assist in nitrogen-fixation and nutrient cycling (Amaranthus et al. 1989).

Ectomycorrhizal fungi.—Ectomycorrhizal (EM) fungi are dependant on specific hosts, while endomycorrhizal fungi can survive in the roots of herbs and shrubs if host trees die. Both types of mycorrhizae may perish if they do not find hosts in $\approx$2 yr (Y. Dalpe, *personal communication*). Seedlings of host trees that land where these fungi have disappeared are not likely to survive. Therefore disruption of the conditions necessary for mycorrhizal survival through intensive management has resulted in aboveground as well as belowground community transition in ecosystems around the world. Woodlands in Africa, perennial grasslands and forests in Western North America, and moist tropical forests have been converted to scrublands and desert as live roots and canopy cover no longer protect the fungi (Perry et al. 1989). Maintaining ecosystem properties such as buried logs will help protect mycorrhizal populations (Harvey et al. 1987). Maser (1988) suggests that declines in long-term productivity and forest die-offs may be partially caused by continued, intensive harvesting, which affects habitats of these fungi.

To use ectomycorrhizal-forming fungi as indicators of forest health, preliminary field work may first have to determine the presence or absence of EM fungi-infected tree roots. The next step may be to compile EM species composition lists for use in the field; however, such a list would not be practical for short-term field surveys since there are hundreds of EM fungal species in a forest system, which may or may not be fruiting at any one time.

Any stand, of course, occurs in a larger landscape context. For example, a forest stand may be isolated within corn fields, or surrounded by other stands. We now move to properties that may be measured within a stand (e.g., large carnivore diversity) but that include landscape characteristics well outside the stand.

8) *Avian community.*—The population levels and number of breeding pairs of a species vary too much regionally to be considered viable characteristics, but species lists or specified levels of richness may be useful properties that reflect forest conditions. Avian richness (i.e., number of species per hectare) is not considered a characteristic of old growth forests. James and Wamer (1982) noted that second-growth forest had equal or greater species diversity than mature second-growth forest. Johnston and Odum (1956) found that species diversity increased through successional seres to the climax stage, but stated that diversity would probably decline in an old-growth hardwood forest because of reduced habitat diversity thanks to a poorly developed understory. The avifauna is nonetheless an essential property of deciduous forest.

Table 10 therefore lists bird species that should occur in mature deciduous forest. Some birds on this list, however, may be found in a variety of habitats (i.e., Black-capped Chickadee, Eastern Wood Pewee), while others tend to be restricted to more mature stands (Ovenbird, Wood Thrush) (Kitchings and Walton 1991).

One way to shorten Table 10 and make it more relevant to our goal is to identify the subset of these species that depend on larger tracts of forest (see Table 11). These species are considered area sensitive (Forman et al. 1976, Galli et al. 1976, Whitcomb et al. 1981, Robbins et al. 1989). It seems that forest size has more of an effect than forest age in predicting bird diversity, particularly for forest interior neotropical migrants. The mechanisms may include a reduction in immigration proportional to patch isolation, a decline in habitat quality through changes in ground moisture levels, and increased predation and brood parasitism associated with forest edges (Robbins 1980, Whitcomb et al. 1981, Kroodsma 1984). Whitcomb et al. (1981) found that neotropical migrants accounted for 80–90% of the breeding species in extensive tracts of Eastern Deciduous Forest but were more rare in small tracts where they constituted less than half of the breeding species. Small forest islands in Maryland, Illinois, Ohio, Delaware, Wisconsin, New Jersey, and Michigan all have similarly poor avifaunal diversity.

TABLE 10. An expected avian community of a mature Eastern Deciduous Forest.

Species†	Study‡ 1	2	3	4	5	6	7
White-breasted Nuthatch (*Sitta carolinensis*)		*	*	*	*	*	*
Ovenbird (*Seiurus aurocapillus*)		*	*	*	*	*	*
Red-eyed Vireo (*Vireo olivaceus*)	*	*	*	*	*	*	*
Wood Thrush (*Hylocichla mustelina*)	*	*	*	*	*		*
Eastern Wood-pewee (*Contopus virens*)	*	*	*	*	*	*	
Hairy Woodpecker (*Picoides villosus*)	*	*	*	*	*	*	
Blue Jay (*Cyanocitta cristata*)	*	*	*	*	*	*	
Black-capped Chickadee (*Parus atricapillus*)			*	*	*	*	
Black-and-white Warbler (*Mniotilta varia*)	*	*	*			*	
Downy Woodpecker (*Picoides pubescens*)	*	*		*	*		
Acadian Flycatcher (*Empidonax virescens*)	*	*			*		*
Tufted Titmouse (*Parus bicolor*)	*	*			*		*
Scarlet Tanager (*Piranga olivacea*)	*			*	*	*	
Great Crested Flycatcher (*Myiarchus crinitus*)	*	*			*	*	
Pileated Woodpecker (*Dryocopus pileatus*)					*	*	*
Veery (*Catharus fuscescens*)				*	*	*	
Ruffed Grouse (*Bonasa umbellus*)				*	*	*	
Hermit Thrush (*Catharus guttatus*)			*	*		*	
Black-throated Blue Warbler (*Dendroica caerulescens*)			*	*		*	
Black-throated Green Warbler (*Dendroica virens*)			*	*		*	
Hooded Warbler (*Wilsonia citrina*)	*	*			*		
Carolina Wren (*Thryothorus ludovicianus*)	*	*					*
Blue-grey Gnatcatcher (*Polioptila caerulea*)	*				*		*
Yellow-billed Cuckoo (*Coccyzus erythropthalmus*)	*	*			*		
Northern Cardinal (*Cardinalis cardinalis*)	*	*					*
Yellow-throated Vireo (*Vireo flavifrons*)	*	*			*		

† The list contains only those species cited in three studies or more.

‡ Study site locations, forest type, and sources: 1. Georgia, *Quercus–Carya* (Johnston and Odum 1956); 2. Maryland, *Liriodendron–Quercus* (Whitcomb et al. 1978); 3. New York, *Acer–Fagus–Betula* (Webb et al. 1977); 4. Ontario, *Acer–Betula* (Martin 1960); 5. Ohio, *Fagus–Acer* (Kendeigh 1944); 6. New York, *Fagus–Acer–Tsuga* (Kendeigh 1956); 7. North Carolina–New York, deciduous (Shugart et al. 1978).

Forests that are second growth or recently logged do not seem to have a poorly developed bird assemblage as long as their area is sufficiently large. Webb et al. (1977) found little difference in the avifaunal composition of a primary stand and those of four selectively logged stands varying in logging intensity. They did find, however, that the populations of some forest interior species declined after logging. The study sites were located within the continuous mature forest of New York's Adirondack Mountains, which probably buffered the stands from any species loss.

Table 11 provides a list of bird species considered characteristic of primary forests. We propose the following three categories: control/normal (≥5 species), intermediate (2–4 species), and low (<2 species).

9) *Large carnivores.*—Large carnivores are another property of Eastern Deciduous Forests. The list of species prior to European settlement would have included the eastern cougar, black bear, fisher, bobcat, red fox, grey fox, and wolf (*Canis lupis* north of 40° latitude, and *Canis rufus* to the south) (Table 12). Hunting pressure and reduced habitat have pushed the eastern cougar to near extinction, and forced the wolf and black bear into smaller or poorer quality habitat. The bobcat and fox appear to have adapted to their fragmented environment, due in part to their smaller habitat requirements. Large carnivores are generally at the top of the food chain; therefore, their presence indicates an intact food web. Some, like the black bear and red fox, help disperse the seeds of trees and shrubs by

TABLE 11. Species from Table 10 that are considered area sensitive.

Species	Study† 1	2	3	4
Ovenbird (*Seiurus aurocapillus*)	*	*	*	*
White-breasted Nuthatch (*Sitta carolinensis*)	*	*	*	*
Black-and-white Warbler (*Mniotilta varia*)	*	*	*	*
Scarlet Tanager (*Piranga olivacea*)	*	*	*	*
Hairy Woodpecker (*Picoides villosus*)	*	*	*	*
Red-eyed Vireo (*Vireo olivaceus*)	*		*	*
Wood Thrush (*Hylocichla mustelina*)	*		*	*
Great Crested Flycatcher (*Myiarchus crinitus*)	*		*	*

† 1. Galli et al. (1976); 2. Whitcomb et al. (1981); 3. Robbins et al. (1989); 4. Forman et al. (1976).

TABLE 12. Large carnivores whose ranges historically included the Eastern Deciduous Forest.

Species*	Mean mass (kg)†		Group size‡	Minimum home range (km²)§
	Male	Female		
Black bear (*Ursus americanus*)	189.9	146.7	1	56.3
Eastern cougar (*Puma concolor*)	183.9	105.9	1	102.4
Wolf (*Canis* sp.)‖	49.5	36.2	7	391.6
Bobcat (*Lynx rufus*)	12.2	9.6	1	30.7
Red fox (*Vulpes vulpes*)	5.2	5.2	3	4.1
Grey fox (*Urocyon cinereoargenteus*)	4.7	4.4	1	1.1
Fisher (*Martes pennanti*)¶	3.9	2.3	1	25.9

* Nomenclature follows Hall (1981).

† Calculated from the maximum and minimum value from Forsyth (1985).

‡ From Gittleman and Harvey (1982).

§ From Gittleman and Harvey (1982), except for eastern cougar, which is from Forsyth (1985).

‖ Historically, two species of wolf were found within the Eastern Deciduous Forest: *Canis lupus* north of 40° latitude, and *Canis rufus* south of 40° latitude (Hall 1981).

¶ Range encompassed most of the Eastern Deciduous Forest range.

consuming their nuts and fruit. Many are carnivores that feed on the numerous herbivores of the forest, thereby keeping the herbivore populations in check. If the herbivore populations were left unchecked, they could drastically alter the forest vegetation composition and relative abundances through overgrazing and browsing. Large carnivores have been explicitly examined in forests in western North America (Ruggiero et al. 1994).

The white-tailed deer is one mammal that has benefited over the years from the absence of large carnivores. Alverson et al. (1988) state that prior to European settlement, northern Wisconsin had relatively low numbers of deer (2–4 deer/km²), but extensive timber cutting in the late 19th century produced excellent habitat for deer. This caused the numbers to soar to ≈14 deer/km² in the 1930s and 1940s, and present day management practices keep it around 2–9 deer/km². High densities of deer can modify forest composition through grazing herbs and browsing young trees. Since forests with inflated numbers of deer are considered altered sites, deer are not included in the list of indicator species. We propose three categories for carnivores: control/normal (≥6 species), intermediate (3–5 species), and low (<3 species).

10) *Forest area.*—Over a few centuries, the forest landscape has been changed from continuous forest to a mosaic of woodlots and the occasional large tract of forest. As a consequence, woodlands have suffered greater losses than any other ecosystem in Southern Ontario (Riley and Mohr 1993). Similar changes have occurred throughout eastern North America. This fragmentation has been shown to alter the species composition, and reduce the species diversity, in the remaining forests (Burgess and Sharpe 1981, McCoy 1982, Freemark and Merriam 1986, Riley and Mohr 1993).

Mammalian and avian species are probably the most affected since they have relatively large territorial requirements. Neotropical migrant birds decline with forest fragmentation, possibly because of a reduction in immigration or a decline in habitat quality (Robbins 1980, Whitcomb et al. 1981, Kroodsma 1984, Freemark and Merriam 1986). Large mammals require large territories (Table 12). For example, a typical pack of timber wolves (*Canis lupis*) requires a home range of nearly 400 km² in the summer, and 800 km² in the winter (Gittleman and Harvey 1982). Similarly, an eastern cougar requires a territory of at least 100 km² (Forsyth 1985).

For a forest to contain the full complement of species, it must be large enough to accommodate those species with the largest area requirements. In fact, the Ontario Ministry of Natural Resources uses the minimum area requirement for a wolf pack to define the necessary size for its wilderness parks (Nudds 1993). The size approximations we shall use are taken from Nudds (1993). He estimates that a forest requires a minimum of 75 ha to contain the full complement of passerines normally found in a contiguous forest. A complete assemblage of mammals requires an area of 100 000 ha. Based on these figures, we propose the following three categories: control/normal ($>10^5$ ha), intermediate (10^2–10^5 ha), and low ($<10^2$ ha).

DISCUSSION

The long-term objectives of such work are to establish quantitative criteria for four purposes: (1) harvesting managed forests in a manner that least alters essential properties of these forests, (2) setting quantitative targets for restoring temperate deciduous forest to original structure and composition, (3) recreating forests on abandoned agricultural land, and (4) locating forest stands that best represent original forests for the establishment of forested ecological reserves.

As a first step toward this goal, we have offered a list of possible forest properties with assigned values derived from the existing literature. There are some obvious limitations. Eastern deciduous forest covers a vast area of North America, and there is obvious variation in species composition and abundance (Braun 1950). In order to assess the eastern deciduous forest than singly. Single properties could be misleading either because of weaknesses in the methods, or because an unusual event has perturbed one aspect of a stand without affecting any of the others. A brief period of grazing can eliminate spring ephemerals, which may require centuries to recover, but the stand may well have other important properties intact. Hence, the entire set of properties, or at least a significant subset of them, must be measured and assessed in conjunction with one another. Each property can be thought of as an axis in *n*-dimensional space, with the distance from the control region to a particular stand being a summary measure of change from natural conditions.

Large-scale natural disturbances like fire and hurricanes may affect some indicator levels. However, we have tried to select properties that will discriminate between natural and human-induced activities, and therefore reflect changes outside the normal envelope of fluctuation (Fig. 3). For example, spring ephemerals are unlikely to be eliminated by a hurricane, yet they are very sensitive to grazing or forest clearing. Similarly, coarse woody debris created by hurricanes will be quite different from coarse woody debris left from whole-tree harvesting or accumulating in managed monocultures. Such figures are speculative, but suggest the manner in which such work could be used.

This work is admittedly coarse scale because we set out to discover some general properties of deciduous forests. Future work could include: (1) addition or deletion of properties (further work on fungi and mycorrhizae is a particular priority); (2) refinement of the quantitative levels assigned to them, particularly the control levels; and (3) calibration for specific forest types. There is much work to be done.

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TABLE 13. Preliminary list of properties and the suggested levels for them.

Property	Measurement	Category values Control	Intermediate	Low
Stand indicators				
1. Tree size	basal area (m^2) per hectare	>29	20–29	<20
2. Canopy composition	proportion of shade-tolerant tree species (American beech, sugar maple, basswood hemlock)	>70%	30–70%	<30%
3. Coarse woody debris	megagrams per hectare	>20	10–20	<10
	presence of large decaying logs (≥8 logs per hectare)	both firm and crumbling	either firm or crumbling	no large logs present
4. Herbaceous layer	number of ephemeral species (see list in Table 5)	≥6	2–5	<2
5. Corticulous bryophytes	number of bryophyte species (not restricted to list in Table 6)	≥7	2–6	<2
6. Wildlife trees	number of snags per 10 ha (>50.8 cm dbh)	≥4	1–3	<1
7. Fungi	no information			
Landscape indicators				
8. Avian community	number of forest interior species	>5	2–4	<2
9. Large carnivores	number of species present	≥6	3–5	<3
10. Forest area	hectares	>10^5	10^2–10^5	<10^2

as a whole, we have kept the properties as large scale and general as possible. We have tried to emphasize macroscale properties that measure essential elements of structure and function rather than search for single indicator species. Future work may be needed to calibrate these coarse-scale properties for individual forest types.

We have emphasized properties for evaluating mesic forest stands. A forest with low indicator values may not necessarily be stressed or degraded, however, it may just be an unusual vegetation type. For example, in the Great Lakes–St. Lawrence forest area, open oak woodlands on southern slopes, cedar woodlands on alvars, and silver maple swamp forests all may score low on some properties. Discretion is always necessary for interpreting observed differences and trends. Evaluation criteria cannot substitute for common sense.

Properties should be considered as a group rather

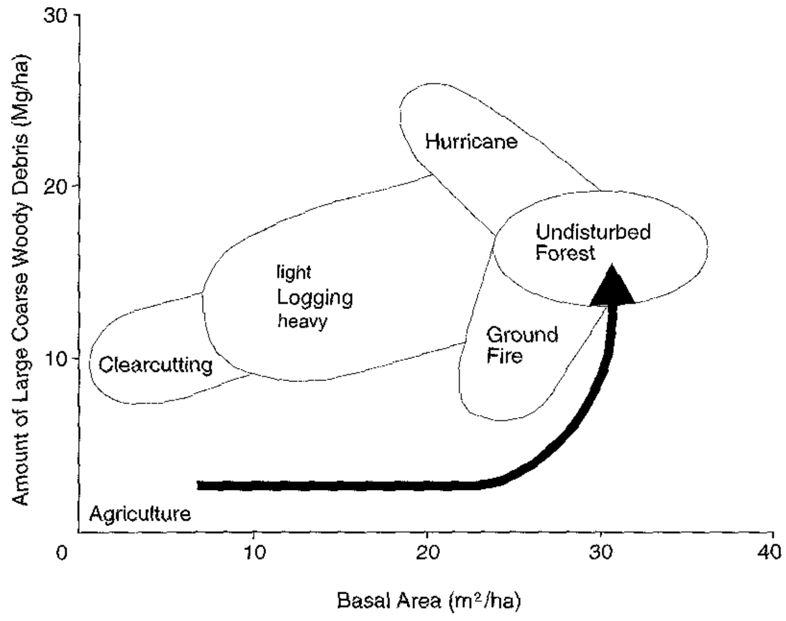

FIG. 3. Suggested changes in two properties of deciduous forests, coarse woody debris and basal area per hectare, with different processes. The arrow indicates a probable time course for the two properties during ecosystem recovery. During recovery/restoration, there is a delay in accumulation of large CWD because it is necessary for biomass to recover in order to create the raw material for CWD.

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