Journal of Tropical Ecology (1996) 12:735–739.

SHORT COMMUNICATION

Abolishing virginity

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KEY WORDS: disturbance, forest ecology, old-growth, succession, tropical rainforest.

In forestry, virginity is relative. – Gary Hartshorn, *personal communication.*

In the last two decades a significant paradigm shift has occurred in the way ecologists describe and study temperate-zone forests. The attempt to define old-growth forests and to measure their structural and functional characteristics has led to substantial progress in the theoretical and practical understanding of these systems (Franklin 1993). A similar shift in terminology and conception has begun in the study of lowland tropical rainforests (= TRF, here defined as Tropical Moist and Tropical Wet forests in the Holdridge system; Holdridge 1979). The purpose of this essay is to encourage this trend. Specifically, I will justify why a shift in conception and terminology is desirable, and suggest a series of readily measured criteria for defining different types of tropical rainforests. I propose that explicitly considering the structural and functional characteristics of forests is an objective and practical method for classifying, comparing and investigating all TRF regardless of their origin.

How do ecologists studying tropical rainforests currently describe old-growth tropical rainforests? I searched the last two years of *Journal of Tropical Ecology*, *Journal of Ecology*, *Ecology* and *Biotropica* and tallied the term first used in all papers on TRF to describe old-growth study sites. In some cases authors merely stated the Holdridge or equivalent classification. In more cases (N = 57), a descriptive term was used to clarify the life zone classification. The most commonly used terms (63%) were 'primary' or 'undisturbed'. Other descriptors included 'mature', 'entirely undisturbed and remote', 'virgin' and 'undisturbed natural'. Only four papers used the term 'old-growth'.

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Table 1. Structural and functional characteristics of lowland tropical rainforests. Secondary forest is defined as forest regenerating after complete clearing (Corlett 1994).

Characteristic	Young secondary forest	Old secondary forest	High-graded or logged forest	Old-growth forest
Stand basal area[(1)]	Lowest	Intermediate	Intermediate	Highest
Distribution of tree stem diameters	Lowest coefficient of variation	Intermediate coefficient of variation	Intermediate coefficient of variation	Highest coefficient of variation
Canopy organization	Even canopy, few gaps[(2)]	Even canopy, gaps more frequent[(3)]	Variable canopy height, small and large gaps common	Variable canopy height, small gaps common but large gaps infrequent
Large lianas and/or epiphytes	Absent	Rare	Variable depending on history	Common
Large logs	Present or absent	Usually absent	Usually present	Aways present
Total quantity of coarse woody debris[(4)]	Usually small	Small	Large	Large
Very large trees (>70 cm diameter above buttresses)[(1)]	Usually absent except as obvious remnants	Usually absent	Usually absent or scarce	Always present at ⩾several per ha[(5)]
Number of tree species with large animal-dispersed seeds with little or no dormancy[(6)]	Few	Some	Many	Many

(1) Saldarriaga *et al.* (1988); (2) Budowski (1965); (3) Saldarriaga & Uhl (1991); (4) Lugo & Brown (1992); (5) Clark & Clark (1995b); (6) Opler *et al.* (1980).

'Undisturbed' was clearly used to mean 'undisturbed by humans', as are parallel terms such as 'pristine', 'virgin' and 'natural'. The meanings of 'primary' and 'mature' are variable. Some authors intended these terms to indicate forests with no known history of human intervention, while others clearly did not, as in 'primary (several centuries old)'.

In practical terms, determining whether or not a forest is now or has ever been affected by human influences is problematic. Given the extremely widespread occurrence of historic (Bush & Colinvaux 1994, Horn & Sanford 1992, Meggers 1994, Piperno 1990, Sanford *et al.* 1985) and recent (Clark & Clark 1995a, Redford 1992) human impacts in the tropics, it seems likely that totally 'virgin' areas are rather rare. And in some very major aspects, all forests world-wide are currently experiencing human impacts from increased CO_2 and other atmospheric and climatic changes (Vitousek 1994).

The current terminology is difficult to apply operationally and offers no ready framework for theoretical and practical comparisons of different tropical forests. I therefore suggest that for initial site descriptions, ecologists focus on a set of easily quantified structural and functional characteristics (Table 1). I consider tropical forests in terms of a continuum ranging from abandoned pastures and agricultural fields to old-growth. This view-point is explicitly comparative in focusing on the gradual accretion of old-growth characteristics over time. Seen this way, forests can be classified and compared by the degree to which they express the properties listed in Table 1. At the old-growth end of this continuum, forests have acquired characteristic structural elements (large lianas and epiphytes, very large trees, heterogeneous tree diameter distribution). Tree regeneration is heavily influenced by tree-fall gaps and large animal-dispersed seeds. At the young end of the scale, forests lack these structural elements and an internal gap dynamic is largely missing. Lightly logged forest is structurally more similar to old-growth than young secondary forests, and high-graded stands grade into old-growth as cutting intensity decreases and/or time since cutting increases.

The characteristics listed in Table 1 are meant to be assessed at spatial scales ranging from small watersheds to large landscapes. The relative expression of these variables is most usefully compared among forests with fairly similar amounts and patterns of precipitation. Forests on non-zonal soils (cf. permanently flooded swamps, white sand soils), areas undergoing primary succession and those subject to landscape-scale disturbances such as hurricanes may not follow this sequence.

Many additional criteria could be used as descriptors of old-growth. For example, every tropical ecologist is familiar with species, genera or families which are maximally abundant at different stages of forest organization (Budowski 1965, Richards 1952, Whitmore 1984). Nevertheless, I purposely avoided using taxonomic criteria to define old-growth. The spectacular taxonomic variation occurring among the great tropical regions defeats my purpose of concentrating on simple, generally applicable variables. The characteristics listed in Table 1 can be assessed relatively quickly and rely on little specialized knowledge. For this reason they lend themselves to widespread usage.

On the other hand, part of the reason for this essay is to stimulate progress in objectively classifying and studying old-growth. There are certainly other readily measured structural and functional variables that vary across the old field–old-growth gradient that I have not considered or that remain to be discovered. Three areas where comparative analyses would be interesting include descriptions of below-ground structure, spatial organization of key resources such as light and soil nutrients (Reiners *et al.* 1994) and individual stem architectures.

Prominent by absence in Table 1 is any mention of tropical forest fauna. There is no question that animals, both vertebrate and invertebrate, play major roles in ecosystem function and may even determine important aspects of TRF structure (Dirzo & Miranda 1991, Redford 1992, Terborgh & Wright 1994). Animal abundances and their relation to human impacts are clearly of great theoretical, practical and conservation interest in tropical forests. However, many issues of major global importance and scientific interest can be addressed at least at a first level by considering only the gross structural and functional aspects of forest vegetation.

In summary, I propose consciously abandoning the concept of 'undisturbed' forest in the tropics. In the light of current knowledge about tropical forests, and given current theoretical and practical research interests, the yardstick of pristine character seems increasingly irrelevant. I propose as a first step classifying TRF's on their gross structure and function, as in Table 1, and with no reference to human impacts. This easily applied level of classification is sufficient to address many important landscape-scale questions. This conceptual framework also set the stage for explicitly considering human effects on systems. Among sites of similar structure and function, what factors are responsible for variance in the abundance of major plant and animal groups? Past or current human effects are one class of such factors. Other major influences include rare megadisturbance events (Meggers 1994, Nelson *et al.* 1994), edaphic factors and biogeographic history.

What a given forest looked like before the actions of indigenous peoples, colonists and global climate change, both secular and historic, may well be unknowable. What is both possible and imperative to understand quickly is the structure and function of a wide variety of existing tropical rainforests. Progress in this direction will come by concentrating on objective and readily quantifiable measures of forest structure and function.

ACKNOWLEDGEMENTS

After years of reading ecological literature I no longer remember the sources of many of these ideas (some may even be original). Anyone who feels that their work is not properly recognized here may well be right. I thank the Andrew

W. Mellon Foundation for financial support, and Deborah A. Clark, Paul Colinvaux, Gary Hartshorn and an anonymous referee for useful critiques.

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Accepted 1 December 1995