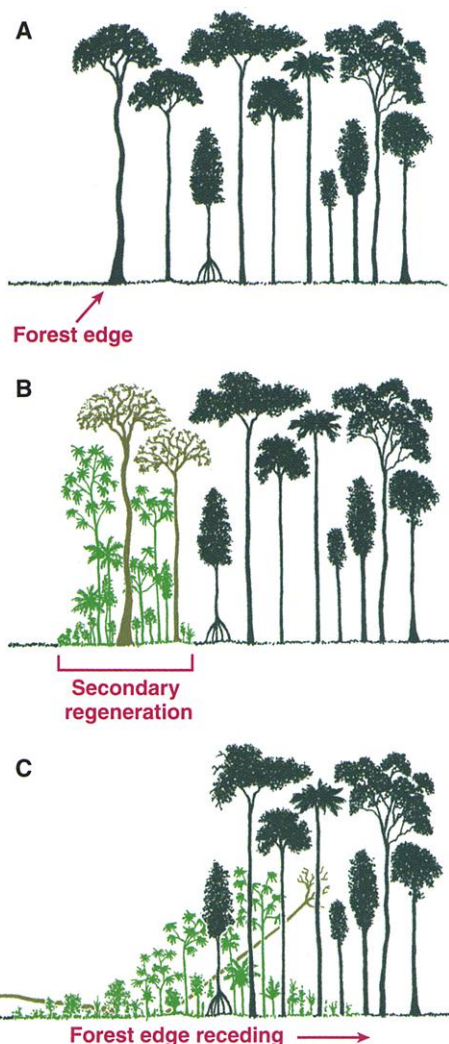


Receding Forest Edges and Vanishing Reserves

Claude Gascon, G. Bruce Williamson, Gustavo A. B. da Fonseca

Logging and road building carve up otherwise intact expanses of forest into small and isolated islands (forest fragmentation), creating a perimeter of abrupt forest edge where ecological changes take place (1). Edge effects in fragments of tropical forest are widespread and complex (1, 2). They have been treated as static phenomena, that is, as a fixed function of edge distance. This has resulted in simplistic landscape management guidelines such as the creation of buffer zones around parks and reserves (3). However, recent research (4) suggests that many tropical landscapes are increasingly experiencing conditions hostile to forest regeneration, including intrusion by fire into areas with a historically low incidence of burning. Furthermore, natural phenomena such as El Niño events act synergistically to magnify the deleterious effects of human disturbance (5). This combination of factors is posing a much more serious threat to forest remnants than previously imagined because forest edges are gradually receding, diminishing the size of fragments and ultimately causing them to collapse inwards. The implications for tropical landscape planning and conservation are far-reaching.

In the first few years, the forest edge allows sunlight and wind to penetrate laterally into the forest fragment (see the figure, this page), resulting in microclimatic changes along a wide band of adjacent forest (6). These changes in turn immediately affect forest structure, leaf fall, turnover in the plant community, seedling recruitment patterns, and distribution of animals (7, 8). Soon tree mortality increases dramatically near the forest edge (2). In the first decade following fragmentation, there is a shift in



The death of a forest. Forest edges at three different stages after isolation. (A) Recent cutover area shows abrupt forest edge subjected to lateral winds and light penetration that allows for significant microclimatic changes inside the forest edge. (B) After several years of isolation, regenerating vegetation is found along the forest border and in the understory, closing the edge. In a landscape with low matrix harshness, this edge will be maintained (and could expand outward), buffering the forest interior from the severity of the initial edge effects. (C) In landscapes with high matrix harshness, the process of forest regeneration along the edge breaks down, resulting in greater penetration of edge effects and a gradually receding edge. The original edge will be replaced by scrubby ruderal vegetation, eventually leading to vanishing reserves.

the arboreal vegetation from climax to pioneer species (that is, a change from tree species characteristic of old-growth to those associated with young, regenerating forests) as conditions favor pioneer life histories (9). Thereafter, the structure of the forest edge changes significantly. In the central Amazon, “closing” of the edge through forest regeneration and primary forest understory growth (10) may act as a buffer against the original edge-induced temperature increases and humidity declines (7) (see the figure, this page).

The distance over which different types of plants and animals or other response variables are affected within a fragment can be important (1, 11, 12). Edge-affected zones as wide as 1 km are not uncommon, and most plant and animal species show detectable impacts up to 100 to 300 m from the forest edge (13). This scale of edge effect implies that fragments up to 1000 hectares will be composed almost entirely of edge-affected habitat (14). In at least one case, edge effects on seedling recruitment permeated a 90,000 hectare tropical rainforest in Borneo (15).

The ability of the regenerating forest along a fragment’s edge to act as a buffer will depend on the “harshness” of the matrix, harshness being defined as the ability of the matrix to degrade the primary forest. (The matrix refers to the intervening variety of habitats in a landscape that surround forest patches). In areas with low matrix harshness, most edge effects will either remain stable over time or decrease as vegetation regenerates along a fragment’s edge. In such cases, normal forest succession occurring at the edge may at least achieve a balance between exposure and regeneration, where the interior of the fragment is buffered and retains most of its primary forest character (7, 8).

Some tropical areas have more severe conditions in the matrix. For example, in the Atlantic Forest of southern Brazil fragments are embedded in huge expanses of sugar cane and *Eucalyptus* plantations where burning and the application of herbicides are routine procedures. The sustainability of such fragments is at risk because the forest is unable to regenerate at the edge or to buffer its interior (9). The result is a pronounced impoverishment (mortality higher than recruitment) of the remaining primary forest interior, with the edge being dominated by a species-poor transition community or weedy vegetation (16, 17).

In the tropics, the most important determinants of matrix harshness are intensity and history of land use, incidence of fire, introduction of exotic species, and

C. Gascon is at the Center for Applied Biodiversity Science, Conservation International, 2501 M Street NW, Suite 200, Washington, DC 20037, USA. G. B. Williamson is in the Department of Biological Sciences, Louisiana State University, 508 Life Sciences Building, Baton Rouge, LA 70803, USA, and Biological Dynamics of Forest Fragments Project, C. P. 478, Instituto Nacional de Pesquisas da Amazônia, 69011-970 Manaus, Amazonas, Brazil. G. A. B. da Fonseca is at the Center for Applied Biodiversity Science, Conservation International, 2501 M Street, NW, Suite 200, Washington, DC 20037, USA, and in the Departamento de Zoologia, Universidade Federal de Minas Gerais, Belo Horizonte, MG 31270, Brazil.

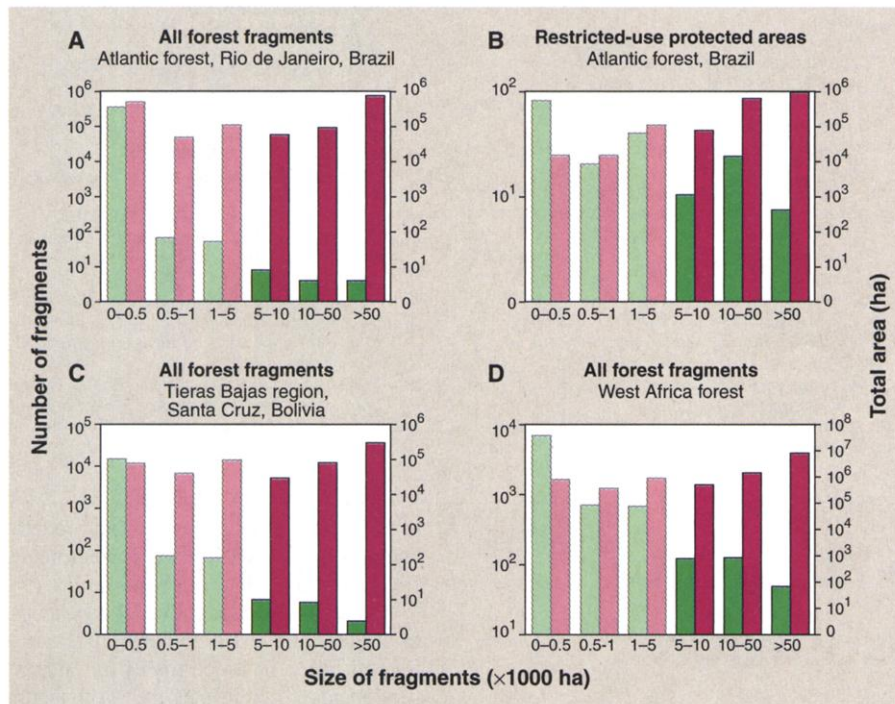
the structure of the matrix vegetation. Fire has played a major role in compounding the impacts of deforestation in the Brazilian Atlantic Forest (18). As Cochrane *et al.* (4) have recently shown, fire is also becoming an important element in Amazonian landscapes through a positive-feedback loop in which recently burned forest becomes much more susceptible to subsequent fires. Fire has a devastating impact on woody plants in wet forests because most tropical tree species have thin bark that makes their stems susceptible to even light surface fires, and they have no underground buds from which to resprout (19).

fire in the Amazon landscape may be sufficient to change regeneration at forest edges into degeneration (from B to C in figure), eventually leading to receding edges and the potential for vanishing fragments.

Increased fire incidence also influences species composition of the regenerating forest in the matrix or along the fragment edge. Here, primary species are replaced by pioneer species that in turn may be eliminated and replaced by exotic or ruderal species, which are more resilient to fire (9, 23). In old fragmented landscapes such as the Atlantic forest of Brazil, native

native species (24). Although invasive species have received much attention in general, their potential importance in fragmented forest landscapes has so far been overlooked. Their success in Hawaii and South Florida bodes poorly for the future of other tropical forests as they become fragmented and exposed to increasing numbers of invasive species.

The field of wildlife management and conservation was born in temperate countries where the maintenance and expansion of forest edges was interpreted as beneficial for game populations and included the prescription of periodic burnings (25). As applied to tropical countries, studies regarding reserve design were the first to address the issue of edges in the planning of protected areas (3), but they largely regarded them as spatially fixed. It is now evident that forest edges should be viewed as a dynamic component of the landscape. Even conventional management guidelines providing buffer zones around protected areas may not, as such, suffice in countering the dynamic nature of forest edges. In order to minimize the foreseeable collapse of many isolated protected areas (9, 26), a landscape-scale conservation strategy is needed. This strategy requires conservationists to



The diminution of fragments. Number and total area of forest fragments in each size class in different tropical regions. Green bars represent the number of fragments and red bars the total area. Pale colors denote the three smaller size classes that are facing serious and immediate risk of receding edges. [Data sources are (A) C. Jenkins, personal communication; (B) Conservation International do Brasil & Sociedade Civil Mamiaráu. Banco de dados das unidades de conservação do Brasil. Conservation International do Brasil, Belo Horizonte, MG (1997); (C) M. K. Steinenger *et al.*, *Conserv. Biol.* (in press); (D) Forest Cover and Protected Areas, WCMC Global Overview of Forest Conservation (1998)].

The increased incidence of accidental and managed burns dramatically affects regeneration along forest edges, resetting succession to time zero (20). Fire also plays an important part in determining the structure and composition of the matrix vegetation (16, 21), which in turn affects tree mortality along fragment edges (22). Worse still, where the edge acts as a conduit to carry fire into the margins of the primary forest, the regenerating forest subsequently proceeds inward, providing a broader band of vegetation susceptible to future incursions of fire (4). Thus, the increased incidence of

tree genera will be replaced by fire-adapted, nonnative shrubs and herbs such as *Lantana*, *Mimosa*, *Stachytarpheta*, *Borreria*, *Lygodium*, and *Hedychium*, as well as fire-adapted grasses. In the Amazon region, where exotics are not as common, tree genera from pioneer-dominated families such as Annonaceae, Cecropiaceae, Clusiaceae, Euphorbiaceae, and Malpighiaceae are favored in the regeneration occurring in cutover (deforested areas) and edge habitat. Exotic animals, such as pigs and Africanized honeybees, as well as plants can cause large-scale damage, resulting in ecological displacement of the

1) maximize the area/perimeter relationship of conservation areas by protecting large forest remnants rather than small ones where possible; by rebuilding connectivity among small adjacent protected areas by setting aside intervening habitat and promoting reforestation of the landscape; and by minimizing perimeter increases due to irregularity in reserve shape;

2) protect the forest edge itself against structural damage, incursion by fire, and colonization by exotics, through leaving a natural buffer zone of forest that could be managed to resemble a natural ecotone (transition from forest to field) rather than an abrupt edge;

3) minimize the harshness of the adjacent matrix by diversifying and promoting less intensive types of land use, controlling the use of fire, minimizing the application of toxic chemicals, and controlling the introduction of exotic plant species.

These objectives are crucial for most postfrontier tropical forest regions (such as, the Atlantic Forest of Brazil, the Philippines and Madagascar), where the landscape is highly fragmented with little or no connectivity between forest remnants. These regions show a size distribution that is highly skewed in favor of forest fragments of smaller size; smaller forest fragments represent a large proportion of the remaining forest in these areas (see figure, this page). For instance, in the Atlantic

Forest of Brazil, the average size of restricted use, protected areas is a mere 9210 hectares, and a significant proportion of the total area and number of remnants are in the small size classes. Even in regions such as the Amazon forest, the deforestation frontier leaves a highly fragmented landscape in its wake (5, 12). Further thwarting conservation efforts are the raging fires that have become epidemic during the dry season, and many parks have experienced repeated incursions by wildfires (18).

Given current knowledge about edge effects, coupled with increasing matrix harshness, we believe that small fragments (<5000 hectares) in most tropical regions are in serious and immediate danger of suffering the receding edge phenomenon. If so, a large proportion of forest remnants in fragmented landscapes that are already protected or available for conservation are doomed to disappear without proper management. Clearly, the future of these reserves demands active and costly management commensurate with the preservation of the last vestiges of tropical ecosystems.

Preemptive planning is necessary to implement conservation on regional and global scales, where such opportunities still exist. For frontier tropical wilderness

areas, the recognition of the dynamic nature of edges demands that conservation planning rapidly migrate to the landscape scale (27). This approach is exemplified by the proposed large-scale biodiversity corridors of the Brazilian rainforests (28) and the Mesoamerican corridor (29). Only through such measures will there be any hope of conserving tropical landscapes and saving forest fragments from a vanishing future.

References

1. C. Murcia, *Trends Ecol. Evol.* **10**, 58 (1995).
2. L. V. Ferreira and W. F. Laurance, *Conserv. Biol.* **11**, 1 (1997).
3. W. F. Laurance and C. Gascon, *Conserv. Biol.* **11**, 577 (1997).
4. M. A. Cochrane *et al.*, *Science* **284**, 1832 (1999).
5. D. C. Nepstad *et al.*, *Nature* **398**, 505 (1999).
6. V. Kapos, *J. Trop. Ecol.* **5**, 173 (1989).
7. C. Gascon and T. E. Lovejoy, *Zool. Analysis of Complex Systems* **101**, 273 (1998).
8. V. Kapos, G. M. Ganade, E. Matsui, R. Victoria, *J. Ecol.* **81**, 425 (1993).
9. V. Viana, A. A. J. Tabanez, J. L. F. Batista, in *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*, W. F. Laurance and R. O. Bierregaard Jr., Eds. (Univ. of Chicago Press, Chicago, 1997), pp. 351-365; W. F. Laurance *et al.*, *Conserv. Biol.* **12**, 460 (1998); M. Tabarelli, W. Mantovani, C. A. Peres, *Biol. Conserv.* **91**, 119 (1999).
10. N. Sizer and E. V. J. Tanner, *Biol. Conserv.* **91**, 135 (1999).
11. W. F. Laurance, S. G. Laurance, P. Delamônica, *Forest Ecol. Manag.* **110**, 173 (1998).
12. D. Skole and C. Tucker, *Science* **260**, 1905 (1993).
13. W. F. Laurance *et al.*, in *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*, W. F. Laurance and R. O. Bierregaard Jr., Eds. (Univ. of Chicago Press, Chicago, 1997), pp. 502-514.
14. W. F. Laurance, *Biol. Conserv.* **69**, 23 (1991).
15. L. M. Curran *et al.*, *Science* **286**, 2184 (1999).
16. G. B. Williamson, R. C. G. Mesquita, K. Ickes, G. Ganade, in *Floresta Amazônica: Dinâmica, Regeneração e Manejo*, C. Gascon and P. Moutinho, Eds. (Instituto Nacional de Pesquisas da Amazônia, Manaus, 1998), pp. 131-144.
17. T. d. S. Filgueiras, *Cadernos de Geociências* **5**, 57 (1990).
18. W. Dean, *With Broadax and Firebrand: The Destruction of the Atlantic Forest* (Univ. of California Press, Berkeley, 1995).
19. C. Uhl and J. B. Kauffman, *Ecology* **71**, 437 (1990).
20. B. G. Williamson and R. C. G. Mesquita, in *Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest*, R. O. Bierregaard Jr., C. Gascon, T. E. Lovejoy, R. C. G. Mesquita, Eds. (Yale University Press, New Haven, in press).
21. J. E. Nichol, *Progress in Environmental Science* **1**, 97 (1999).
22. R. C. G. Mesquita, P. Delamônica, W. F. Laurance, *Biol. Conserv.* **91**, 129 (1999).
23. J. J. Parsons, *J. Range Manag.* **25**, 12 (1972); M. A. Cochrane and M. D. Schulze, *Biotropica* **31**, 2 (1999).
24. M. Enserink, *Science* **285**, 1834 (1999).
25. A. Leopold, *Game Management* (Scribner's, New York, 1933).
26. W. F. Laurance *et al.*, *Science* **278**, 1117 (1997).
27. M. E. Soulé and J. Terborgh, *Continental Conservation: Scientific Foundations of Regional Reserve Networks* (Island Press, Washington, 1999).
28. M. J. Ayres *et al.*, *Os Corredores Ecológicos das Florestas Neotropais do Brasil, Projeto Parques e Reservas (PP-G7)* (Ministério do Meio Ambiente, IBAMA, Banco Mundial, 1997).
29. A. Vega, *Corredores Conservacionistas en la Región Centroamericana: Memórias de una Conferencia Regional* (Tropical Research and Development, Inc., Gainesville, FL, 1994).

PERSPECTIVES: STRUCTURAL BIOLOGY

A Chloride Pump at Atomic Resolution

John L. Spudich

Membrane proteins are involved in selective transport across the cell membrane and the sensing and transmission of information from the extracellular environment to the cell interior. In *Halobacterium salinarum*, both transport and sensory signaling are accomplished by a family of four archaeal rhodopsins, homologous proteins that are modifications of a common design. The proteins each contain seven membrane-embedded helices with a conserved interior binding pocket surrounding a retinal prosthetic group (1-3). Photochemical reaction cycles similar in early steps are induced by retinal photoisomerization in each of the four proteins but have distinctly different outcomes. On page 1390 of

this issue, Kolbe *et al.* (4) report a new structure that sheds light on how proton and chloride transport mechanisms are related in different members of this family.

Bacteriorhodopsin uses light to power transport of a proton from the cytoplasm to the extracellular medium (see the figure). Halorhodopsin is also a light-driven ion pump but has different specificity and acts in the opposite direction, moving a chloride ion from the extracellular medium into the cell cytoplasm. The resulting electrochemical ion gradients provide a source of energy to the cell and enable pH control. The sensory rhodopsins (SRI and SRII) are phototaxis receptors. Each of them is a subunit of a signaling complex that includes a transducer protein (HtrI and HtrII) that controls a phosphorylation cascade modulating the flagellar motors. Numerous homologs of these proteins have been found in other haloarchaea. A eukaryotic photoactive homolog, exhibit-

ing a very similar photochemical reaction cycle to that of SRII, has also been identified in the fungus *Neurospora crassa* (5).

Experiments that convert one function to another suggest a common mechanism for the different functions of the archaeal rhodopsins. At acid pH, the proton pump bacteriorhodopsin transports chloride (6), and in the presence of azide the halide pump halorhodopsin transports protons (7). Moreover, a single mutation, Asp⁸⁵ → Thr, converts bacteriorhodopsin into a chloride pump with halorhodopsin-like photochemical reactions (8). Separation from its tightly bound transducer HtrI subunit converts SRI from a sensory to a transport rhodopsin, which pumps protons across the membrane in the same direction as does bacteriorhodopsin. HtrI interacts with SRI by transmembrane helix-helix contacts (9) and inhibits the pump by closing SRI's cytoplasmic proton channel (10).

To elucidate the underlying molecular mechanism that confers this multiplicity of basic membrane functions on variants of a single evolutionary progenitor protein, we need atomic resolution structures of the proteins in the dark and in their light-activated forms. Bacteriorhodopsin was first visualized by electron crystallographic analysis of two-dimensional (2D) crystals

The author is in the Department of Microbiology and Molecular Genetics, University of Texas-Houston Medical School, Houston, TX 77030, USA. E-mail: spudich@utmsi.med.uth.tmc.edu