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Teja Tscharntke, Christoph Leuschner,
Manfred Zeller, Edi Guhardja,
Arifuddin Bidin
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Stability of Tropical Rainforest Margins

Linking Ecological, Economic and Social Constraints of Land Use and Conservation

With 89 Figures, 1 in colour

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Editors:

Prof. Dr. Teja Tscharntke
Agroecology Group
University of Göttingen
Waldweg 26,
37073 Göttingen, Germany
E-mail: ttschar@gwdg.de

prof. Dr. Manfred Zeller
Institute of Agricultural Economics
and Social Sciences in the Tropics and
Subtropics, University of Hohenheim
(490)
70593 Stuttgart, Germany
E-mail:
manfred.zeller@uni-hohenheim.de

Prof. Dr. Christoph Leuschner
Department of Plant Sciences
University of Göttingen
Untere Karspüle 2
37073 Göttingen,
Germany
E-mail: cleusch@gwdg.de

Prof. Dr. Edi Guhardja
Center for Tropical Forest Margin,
Institut Pertanian Bogor (IPB), Jl.
Raya Gunung Gede, Bogor 16153,
Indonesia
E-mail: storma-ipb@indo.net.id

Dr. Arifuddin Bidin
Universitas Tadulako, Kampus
Bumi Tondo, Palu 94118,
Indonesia
E-mail: storma-palu@gwdg.de

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Contents

List of Contributors

Melani Abdulkadir-Sunito
Department of Communication and Community Development, Faculty of Human Ecology, Bogor Agricultural University, Indonesia

Tatiana Deane de Abreu Sá
Empresa Brasileira de Pesquisa Agropecuária, Embrapa Sede, Parque Estação Biológica - PqEB s/n., Brasília-DF, - Brazil - CEP 70770-901

Diógenes S. Alves
Instituto Nacional de Pesquisas Espaciais (INPE), Av dos Astronautas 1758, CEP 12227-010 São José dos Campos SP, Brazil

M. Amran Amir
Institute of Forest Management, Faculty of Agriculture, Bumi Tondo Campus, Tadulako University, Palu 94118, Indonesia

Iswandi Anas
Laboratory of Soil Biology, Soil Department, Faculty of Agriculture, Institut
Pertanian Bogor (IPB), Darmaga Campus, Bogor 16680, Indonesia

Muhammad Ardiansyah
Institute of Soil Sciences, Bogor Agricultural University (IPB), Bogor, Indonesia

Hadi Susilo Arifin
Department of Landscape Architecture, Faculty of Agriculture, IPB, Bogor, Indonesia

Inge Armbrecht
Departamento de Biología, Universidad de Valle, Apartado Aéreo 25360, Cali, Colombia

Jan Barkmann
Junior Scientist Group "Economic Valuation of Ecosystem Functions and Services" and Environmental and Resource Economics, Department of Agricultural Economics and Rural Development, University of Göttingen, Platz der Göttinger Sieben 7, D-37073 Göttingen, Germany

Pablo C. Benítez
Department of Economics, University of Victoria, PO Box 1700 STN CSC, Victoria BC V8W 2Y2, Canada

Arifuddin Bidin
Universitas Tadulako, Kampus Bumi Tondo, Palu 94118, Indonesia (Sulteng)

Regina Birner
International Food Policy Research Institute (IFPRI), Washington, D.C., USA

Jan Börner
Center for Development Research (ZEF), University of Bonn, Walter-Flex-Str. 3, 53113 Bonn, Germany

Merijn M. Bos
Institute of Agroecology, University of Göttingen, Waldweg 26, D-37073 Göttingen, Germany

Gunnar Brehm
Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum, University of Jena, Erbertstrasse 1, 07745 Jena, Germany

Damayanti Buchori
Department of Pest and Plant Diseases, Faculty of Agriculture IPB, Bogor Agricultural University, Jl. Kamper Kampus, IPB Darmaga, Bogor 16680, Indonesia

Boris Büche
Agroecology, University of Göttingen, Waldweg 26, D-37073 Göttingen, Germany

Manfred Denich
Center for Development Research (ZEF), University of Bonn, Walter-Flex-Str. 3, 53113 Bonn, Germany

Thomas V. Dietsch
Institute of the Environment, Center for Tropical Research, University of California, Los Angeles, La Kretz Hall, Suite 300, Box 951496, Los Angeles, California 90095-1496, USA

Johannes Dietz
Tropical Silviculture, Institute of Silviculture, University of Göttingen, Büsgenweg 1, 37077 Göttingen, Germany and
Plant Ecology, Albrecht-von-Haller-Institute of Plant Sciences, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany

Stefan Erasmi
Institute of Geography, Department of Cartography, GIS and Remote Sensing, University of Göttingen, Goldschmidtstr. 5, 37077 Göttingen, Germany

Raffael Ernst
Department of Animal Ecology and Tropical Biology, Biocenter University of Würzburg, Am Hubland 97074 Würzburg, Germany

Ulrike Falk
Institute of Bioclimatology, University of Göttingen, Büsgenweg 2, Göttingen, Germany

Heiko Faust
Department of Cultural and Social Geography, Institute of Geography, University of Göttingen, Goldschmidtstr. 5, D-37077 Göttingen, Germany

Konrad Fiedler
Department of Population Ecology, University of Vienna, Althanstrasse 14, 1090 Vienna, Austria

Klaus Glenk
Junior Scientist Group "Economic Valuation of Ecosystem Functions and Services" and Environmental and Resource Economics, Department of Agricultural Economics and Rural Development, University of Göttingen, Platz der Göttinger Sieben 7, D-37073 Göttingen, Germany

S. Robbert Gradstein
Institute of Plant Sciences, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany

Gode Gravenhorst
Institute of Bioclimatology, University of Göttingen, Büsgenweg 2, Göttingen, Germany

Stefan Grote
Institute of Bioclimatology, University of Göttingen, Büsgenweg 2, Göttingen, Germany

Edi Guhardja
Kampus IPB Baranang Siang, Ex-Aula Kantor Pusat, Institut Pertanian Bogor, JL Raya Pajajaran, Bogor 16144, Indonesia (Jabar)

Handian Handi
Laboratory for Social Forestry, Faculty of Forestry, Institute Pertanian Bogor, Bogor, Indonesia

Marieke Harteveld
Plant Ecology, Albrecht-von-Haller-Institute of Plant Sciences, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany

Bettina Hedden-Dunkhorst
Federal Agency of Nature Conservation (BfN), Konstantinstr. 110, 53179 Bonn, Germany

Dietrich Hertel
Plant Ecology, Albrecht-von-Haller-Institute of Plant Sciences, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany

Nadine Hilt
Chair of Animal Ecology I, University of Bayreuth, 95440 Bayreuth, Germany

Patrick Höhn
Agroecology, University of Göttingen, Waldweg 26, D-37073 Göttingen, Germany

Dirk Hölscher
Tropical Silviculture, Institute of Silviculture, University of Göttingen, Büsgenweg 1, 37077 Göttingen, Germany

Andreas Ibrom
Institute of Bioclimatology, University of Göttingen, Büsgenweg 2, Göttingen, Germany and
Risø National Laboratory, Frederiksborgvej 399, DK-4000 Roskilde, Denmark

Tania June
Southeast Asian Ministers of Education Organization Regional Centre for Tropical Biology (SEAMEO BIOTROP), BTIC Building, Jl. Raya Tajur Km.6, Bogor, Indonesia and
Faculty of Mathematics and Natural Resources, Bogor Agricultural University/SEAMEO BIOTROP, Bogor, Indonesia

Martin Kappas
Institute of Geography, Department of Cartography, GIS and Remote Sensing, University of Göttingen, Goldschmidtstr. 5, 37077 Göttingen, Germany

Katja Kehlenbeck
Department of Crop Sciences: Tropical Crops, University of Göttingen, Grisebachstr. 6, D-37077 Göttingen, Germany

Alwin Keil
Institute of Agricultural Economics and Social Sciences in the Tropics and Subtropics, University of Hohenheim (490), D-70593 Stuttgart, Germany

Michael Kessler
Institute of Plant Sciences, University of Göttingen, Untere Karspüle 2, 37073
Göttingen, Germany

Alexandra-Maria Klein
Agroecology, University of Göttingen, Waldweg 26, D-37073 Göttingen, Germany

Heiner Kreilein
Institute of Bioclimatology, University of Göttingen, Büsgenweg 2, Göttingen, Germany

Werner Kreisel
Department of Cultural and Social Geography, Institute of Geography, University of Göttingen, Goldschmidtstr. 5, D-37077 Göttingen, Germany

William F. Laurance
Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panamá and Biological Dynamics of Forest Fragments Project, National Institute for Amazonian Research (INPA), C.P. 478, Manaus, AM 69011-970, Brazil

Christoph Leuschner
Plant Ecology, Albrecht-von-Haller-Institute of Plant Sciences, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany

K. Eduard Linsenmair
Department of Animal Ecology and Tropical Biology, Biocenter University of Würzburg, Am Hubland 97074 Würzburg, Germany

Brigitte L. Maass
Department of Crop Sciences: Tropical Crops,
University of Göttingen, Grisebachstr. 6, D-37077 Göttingen, Germany

Adam Malik
Institute of Forest Management, Faculty of Agriculture, Bumi Tondo Campus, Tadulako University, Palu 94118, Indonesia

Sulaiman Mamar
Department of Anthropology, Universitas Tadulako, Kampus Bumi Tondo, Palu 94118, Indonesia

Rainer Marggraf
Environmental and Resource Economics, Department of Agricultural Economics and Rural Development, University of Göttingen, Platz der Göttinger Sieben 7,
D-37073 Göttingen, Germany

Arisbe Mendoza-Escalante
Center for Development Research (ZEF), University of Bonn, Walter-Flex-Str. 3, 53113 Bonn, Germany

Johannes Merklein
Institute of Bioclimatology, University of Göttingen, Büsgenweg 2, Göttingen, Germany

Sonja Migge-Kleian
Ecology Group, Institute of Zoology, University of Göttingen, Berliner Strasse 28, 37073 Göttingen, Germany

Roland Olschewski
Institute of Forest Economics, University of Göttingen, Büsgenweg 5, D-37077 Göttingen, Germany

Alexander Oltchev
Institute of Bioclimatology, University of Göttingen, Büsgenweg 2, Göttingen, Germany and A.N.Severtsov Institute of Ecology and Evolution of the Russiona Acadamy of Sciences (RAS), 33 Leninskiy Prosp., Moscow 119071, Russia

Elise Pendall
Department of Botany, 1000 E. University Ave., University of Wyoming, Laramie, WY 82071, USA

Ivette Perfecto
School of Natural Resources and Environment, Dana Building, University of Michigan, 440 Church St. Ann Arbor, MI 48109, USA

Stacy M. Philpott
Smithsonian Migratory Bird Center, National Zoological Park, 3001 Connecticut Avenue NW, Washington, DC 20008, USA

Ramadhanil Pitopang
Department of Forest Managament and Herbarium Celebense, Tadulako University, Palu, Indonesia

Catherine Potvin
Department of Biology, McGill University, 1205 Docteur Penfield, Montreal, Quebec H3A 1B1, Canada

Golam Rakkibu
Institute of Bioclimatology, University of Göttingen, Büsgenweg 2, Göttingen, Germany

Abdul Rauf
Tadulaku University (UNTAD), Kampus Bumi Tadulako Tondo, Palu - 94118, Indonesia

Mark-Oliver Rödel
Department of Animal Ecology and Tropical Biology, Biocenter University of Würzburg, Am Hubland 97074 Würzburg, Germany

Thomas Ross
Institute of Bioclimatology, University of Göttingen, Büsgenweg 2, Göttingen, Germany

Shahabuddin Saleh
Faculty of Agriculture, University of Tadulako, Kampus Bumi Tadulako Tondo, Palu-Indonesia

Klas Sander
Forest Economist, Environment Department, The World Bank, 1818 H Street NW, Washington DC, USA

Matthias Schaefer
Ecology Group, Institute of Zoology, University of Göttingen, Berliner Strasse 28, 37073 Göttingen, Germany

Björn Schippers
Department of Cultural and Social Geography, Institute of Geography, University of Göttingen, Goldschmidtstr. 5, D-37077 Göttingen, Germany

Wenke Schulz
Ecology Group, Institute of Zoology, University of Göttingen, Berliner Strasse 28, 37073 Göttingen, Germany

Christian H. Schulze
Department of Population Ecology, University of Vienna, Althanstrasse 14, 1090 Vienna, Austria

Stefan Schwarze
Institute of Rural Development, University of Göttingen, Waldweg 26, D-37073 Göttingen, Germany

Luitgard Schwendenmann
Tropical Silviculture, Institute of Silviculture, University of Göttingen, Büsgenweg 1, 37077 Göttingen, Germany

M.T.Felix Sitorus
Department of Communication and Community Development, Faculty of Human Ecology, Bogor Agricultural University, Indonesia

Lorena Soto-Pinto
El Colegio de la Frontera Sur, Unidad San Cristóbal, Carretera Panamericana y Periférico Sur, Apartado Postal 63. C.P. 29290, San Cristóbal de las Casas, Chiapas, México

Ingolf Steffan-Dewenter
Agroecology, University of Göttingen, Waldweg 26, D-37073 Göttingen, Germany

Andrea Steingrebe
Ecology Group, Institute of Zoology, University of Göttingen, Berliner Strasse 28, 37073 Göttingen, Germany

Leti Sundawati
Laboratory for Social Forestry, Faculty of Forestry, Institute Pertanian Bogor, Bogor, Indonesia

Endriatmo Sutarto
Department of Agricultural Socio-Economic Sciences, Institut Pertanian Bogor, Jl. Raya Pajajaran, Bogor 16143, Indonesia

Raquel Thomas
Iwokrama International Centre for Rain Forest Conservation and Development, 77 High Street, Kingston, Georgetown, Guyana

Teja Tscharntke
Agroecology, University of Göttingen, Waldweg 26, D-37073 Göttingen, Germany

André Twele
Institute of Geography, Department of Cartography, GIS and Remote Sensing, University of Göttingen, Goldschmidtstr. 5, 37077 Göttingen, Germany

Adhitya Wardhono
Institute of Rural Development, University of Göttingen, Waldweg 26, D-37073 Göttingen, Germany

Robert Weber
Department of Cultural and Social Geography, Institute of Geography, University of Göttingen, Goldschmidtstr. 5, D-37077 Göttingen, Germany

Maria Wiens
Plant Ecology, Albrecht-von-Haller-Institute of Plant Sciences, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany

Jan-Patrick Witte
Landscape Ecology, Institute of Geography, University of Göttingen, Goldschmidtstr. 5, D-37077 Göttingen, Germany and Environmental and Resource Economics, Department of Agricultural Economics and Rural Development, University of Göttingen, Platz der Göttinger Sieben 7, D-37073 Göttingen, Germany

Lars Woltmann
Ecology Group, Institute of Zoology, University of Göttingen, Berliner Strasse 28, 37073 Göttingen, Germany

Manfred Zeller
Institute of Agricultural Economics and Social Sciences in the Tropics and Subtropics, University of Hohenheim (490), D-70593 Stuttgart, Germany

The stability of tropical rainforest margins, linking ecological, economic and social constraints of land use and conservation – an introduction

Teja Tscharntke[1], Christoph Leuschner[2], Manfred Zeller[3], Edi Guhardja[4], and Arifuddin Bidin[5]

[1] Agroecology, University of Göttingen, Waldweg 26, D-37073 Göttingen, Germany
[2] Plant Ecology, Albrecht-von-Haller-Institute for Plant Sciences, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany
[3] Rural Development Theory and Policy, Institute of Agricultural Economics and Social Sciences in the Tropics and Subtropics, University of Hohenheim (490a), 70593 Stuttgart, Germany
[4] Kampus IPB Baranang Siang, Ex-Aula Kantor Pusat, Institut Pertanian Bogor, JL Raya Pajajaran, Bogor 16144, Indonesia (Jabar)
[5] Universitas Tadulako, Kampus Bumi Tondo, Palu 94118, Indonesia (Sulteng)

Tropical rainforests disappear at an alarming rate causing unprecedented losses in biodiversity and ecosystem services (Hughes et al. 1997, Noble & Dirzo 1997, Tilman et al. 2001, Achard et al. 2002) with Southeast Asia showing the highest rates of deforestation of any major tropical region (Sodhi et al. 2004). Despite an increased recognition of the value of these goods at national and international levels, rainforests continue to be seriously threatened by various forms of encroachments such as low-intensity harvesting of non-timber forest products by the rural poor, large-scale plantation forestry by the state or private actors, and the conversion of forested land by smallholder farmers. Transformation of ecosystems and changes in land use affect important ecosystem services and ultimatively human well-being (Robertson & Swinton 2005).

The stability of rainforest margin areas has been identified as a critical factor in the preservation of tropical forests (Müller & Zeller 2002, Maertens et al. 2006). These areas include the forest edge zone and the belt of agricultural land use systems, which is usually surrounding the forests. Stability has an ecological, social and economic dimension, and understanding the multidisciplinary nature of land use change in tropical rainforest margins is the key to identify more suitable development objectives, such as mitigation of climate change effects and biodiversity loss, poverty reduction, and economic development of rural areas (Vosti & Reardon 1997, Balmford et al. 2002, Totten et

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al. 2003, Bawa et al. 2004, Steffan-Dewenter et al. 2006). Rainforest margins are far from stable with respect to social, economic and ecological properties. The challenge is to provide policy-relevant knowledge, based on an integrated scientific approach, to counteract destabilizing processes at different spatial and temporal scales, from the intra-household, household and village level to landscapes and regions.

The global human population is expected to increase further in the near future with the inevitable consequence of an expansion and intensification of agriculture and the associated destructive environmental impacts (Tilman et al. 2001, 2002, Foley et al. 2005). These impacts will particularly happen in regions where agricultural intensification is a relatively recent process such as in the humid tropics (Matson et al. 1997). Currently, too little is known about how to control this process and to identify trade-offs as well as synergies of land use and conservation (Robertson & Swinton 2005). Land use systems need management decisions based on the assessment of environmental costs and benefits and a thorough knowledge of ecosystem properties. These include the evaluation of local land-use practices in the forest (Sodhi et al. 2004), intensification in agroecosystems (Perfecto et al. 2005) and the assessment of alternative land-use options with concepts and data-driven models of large-scale land-use change in tropical, human-dominated landscapes (Laurance 2001). A particular challenge is to show how nature reserves contribute to the adaptive capacity of regional land-use matrices (du Toit et al. 2004) and to develop management schemes for tropical landscapes under the consideration of multiple ecosystem services, not just marketable commodities (Robertson & Swinton 2005).

This edited book provides a platform for scientists from socio-economic and natural sciences interested in the use and conservation of tropical rainforest resources. The research papers aim to contribute to an improved understanding of the processes that have stabilizing or destabilizing effects on ecological and socio-economic systems of tropical rain forest margins and include interdisciplinary papers that strive to integrate environmental, technological and socio-economic issues. The book features three interconnected thematic foci of interdisciplinary research, i.e. forest use and forest disturbance, agroforestry management and integrated land-use concepts.

Part 1: Ecological and socio-economic impacts of different forest use intensities

Forest use intensities greatly differ with respect to ecological and socio-economic benefits and costs. The income and utility derived from different types of forest use varies by socio-economic group differentiated by wealth, ethnicity, education, and other criteria. Responses of biodiversity and ecosystems functions greatly differ with organism group considered, making generalizations difficult.

William F. Laurance summarizes key findings of the Biological Dynamics of Forest Fragments Project in Amazonia, the world's largest and longest-running experimental study on habitat fragmentation. Edge effects play a key role in fragment dynamics and the surrounding matrix has a major influence on fragment connectivity and functioning. Many Amazonian species avoid even small clearings.

Konrad Fiedler et al. focus on tropical forest moths and their response to forest disturbance and recovery. Using large data sets from Borneo and Ecuador, they found strong responses of species composition to disturbance, but not always of species diversity. Beta, rather than alpha, diversity appeared to be meaningful to assess land use impacts.

Raffael Ernst et al. present results on amphibian communities in disturbed forests of the Neo- and Afrotropics. Patterns in community composition, and hence beta diversity, is a key in understanding impacts of human disturbance. These authors argue that alterations in the functional diversity of amphibians are a good predictor of habitat change.

Dietrich Hertel et al. address the effects of forest use and forest conversion on the below-ground compartment in the wet tropical forests of Sulawesi (Indonesia). The authors review the response of fine root biomass to forest disturbance intensity and interpret results with respect to carbon storage in the root system.

Luitgard Schwendenmann et al. present data on how forest conversion affects soil carbon pools, carbon mineralization rates and soil respiration in Central Panama. The active soil organic carbon pool was found to be a sensitive indicator of soil respiration and may indicate land-use changes.

Johannes Dietz et al. analyze how low-intensity forest use in Sulawesi (Indonesia) influences forest structure. They found a higher interception loss in taller stands. Forest management, even at low or moderate intensities, had a significant impact on forest structural parameters and associated ecosystem functioning such as rainfall partitioning in the canopy.

Sonja Migge-Kleian et al. review the driving factors for soil and litter arthropod communities that are influenced by land-use intensification in rainforest margins. Changes in soil/litter moisture and temperature become very important, leading to reduced richness in drier environments. In an experimental study in Sulawesi (Indonesia), the diversity of soil-dwelling species showed a variable response to land-use changes. Disturbance-mediated changes in diversity also include functional changes of the soil/litter communities.

Melani Abdulkadir-Sunito and M. T. Felix Sitorus relate land-use and forest encroachment patterns to ethnicity in Sulawesi (Indonesia). This case study shows social constraints of inter-ethnic relations and land-use systems. Forest encroachment is not only perceived as an economic, but also as an ethno-political action.

Barkmann et al. assess economic preferences for biodiversity and ecosystems services, including the endemic dwarf buffalo "anoa", the preponderance of shading trees in cacao plantations, and the availability of water and rattan.

The local demand for these environmental non-market services, established by choice experiments, does not suffice to compensate financial benefits from rainforest conversion or agroforestry intensification that accrue to individual households.

Stefan Schwarze et al. quantify the contribution of forest products to household incomes in Sulawesi (Indonesia) and investigate links between poverty, livelihood systems and extraction of forest products. Forest products, especially rattan, were a main source of income for the poorest households, while a village agreement could be shown to have a strong negative influence on the likelihood of selling forest products.

Part 2: Sustainable management of agroforestry systems

Most tropical landscapes are highly fragmented and harbor a mosaic of different land use systems. Low-intensity agroforestry may support high biodiversity stabilizing ecosystem functioning, in particular when shaded by natural trees and neighbored by natural forest (Tscharntke et al. 2005). In contrast, high-intensity agroforestry with mono-dominant, planted shade trees and in a monotonous landscape matrix may be characterized by less environmental benefits and high agrochemical inputs. In this second part of the book, the ecological and socio-economic benefits of different agroforest management practices will be compared and related to patterns and processes in natural forests.

Ivette Perfecto et al. evaluate the contribution of traditionally grown shade coffee to the social and ecological stability of Northern Latin America. These agroforestry systems maintain a high biodiversity that in turn contributes to agroecosystem functioning. Coffee certification programs help to sustain important ecological functions such as biological control and carbon sequestration.

Roland Olschewski et al. present an example of how economic valuations of ecosystem services may contribute to the stability of rainforest margins. In a study of coffee bee pollination and pest control from Sulawesi (Indonesia), they quantify the dependence of the farmers' net revenues on the distance of agroforests to natural forests, which provide nesting sites for bees. The promotion of certified "biodiversity-friendly" coffee may enhance rainforest preservation within a mosaic of competing land-use options.

Merijn Bos et al. provide data on the response of insect diversity to rainforest conversion in Sulawesi (Indonesia). Shaded agroforestry systems may still support high diversity levels of beetles, ants, bees, wasps, and dung beetles, and agroforests should be included in conservation plans at the landscape level.

Katja Kehlenbeck et al. describe the plant diversity in the traditional, complex Indonesian homegardens, which are important for subsistence pro-

duction in rural areas. Homegardens are found to integrate socioeconomic and ecological advantages.

S. Robbert Gradstein et al. studied in Sulawesi (Indonesia) how tree diversity is related to human land use. Roughly one third of tree species in the rainforest (51-63 per 0.25 ha) were important as commercial timber trees, while tree diversity was little affected by moderate land use, but greatly reduced in cacao agroforestry.

Jan Börner et al. evaluate alternatives to slash-and-burn in forest-based fallow systems of eastern Amazonia. These include mulching for the management of soil organic matter and fire-free land clearing with bush choppers and enrichment plantings using fast-growing leguminous tree species. However, costs of mulching are high and taxes are promising policy options to promote fire-free land preparation techniques.

Klas Sander and Manfred Zeller conclude from a case study in Madagascar that the poorest households suffer most from a strict forest conservation approach, while better-off households with more irrigated agricultural land benefit more due to an improved provision of indirect forest services, particularly watershed protection. Furthermore, they discuss the implementation of incentives for afforestation at the household level and management strategies to meet the increasing direct demand on forest resources.

Part 3: Integrated concepts of land use in tropical forest margins

Rain forest margin areas comprise a wealth of land-use systems with different levels of agricultural intensification, from simplified annual crops to highly complex agroforestry systems (Schulze et al. 2005). This part of the book aims to contribute to a better understanding of the dynamics of land use change and related changes in resource availability under various policy scenarios to create improved strategies to reduce and potentially reverse degradation processes.

Alwin Keil et al. analyze the potentials to reduce deforestation by enhancing the technical efficiency of crop production in agroecosystems of the forest margin area. Based on data from Sulawesi (Indonesia), the authors conclude that improvement of technical efficiency may reduce deforestation by increasing incomes on already converted land, but there is also the need to control the influx of migrants attracted by the profitability of higher productivity.

Robert Weber et al. relate ethnicity and migration as cultural impact factors to land-use change in rainforest margins of Sulawesi (Indonesia). The results show a change from a food-first to a cash crop-first strategy, driven by a distinct, immigrating ethnic group (the Bugis) introducing improved knowledge of agricultural intensification.

Stefan Erasmi et al. discuss the state of the art of data analyses for the assessment of land-cover changes in the tropics. Satellite image-based land

cover classifications uncover a large inconsistency regarding land cover. The authors suggest improvements for better technical and conceptual monitoring systems.

Andreas Ibrom et al. apply a series of models to predict net primary production from regional meteorological and remote sensing data of a rainforest margin area of Sulawesi (Indonesia). Scenarios suggest that carbon dioxide sequestration and total evaporation increase and sensible heat fluxes and surface temperatures decrease with land-use intensification.

Diogenes S. Alves analyzes deforestation processes in the Brazilian Amazon. Based on the results of four major research programs, he concludes that the tasks of reducing and mitigating deforestation impacts and fostering sustainable land use are not to be engineered but, rather, negotiated, which is a major challenge for science and technology.

Most chapters of this book were presented at an international symposium held at the Georg-August-University of Goettingen in September 2005. The editors thank the four coordinators of the Collaborative Research Center SFB 552 "STORMA" ("Stability of Rainforest Margins in Indonesia"), Daniel Stietenroth, Wolfram Lorenz, Surya Tarigan and Adam Malik, for their invaluable support, Jan Barkmann for the handling of several manuscripts and many peers for their thoughtful reviews. Technical assistance during the editorial process was provided by Stella Aspelmeier. The financial support by the German Science Foundation (the Deutsche Forschungsgemeinschaft DFG) is gratefully acknowledged.

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Ecosystem decay of Amazonian forest fragments: implications for conservation

William F. Laurance[1,2]

[1] Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panamá Email: laurancew@si.edu
[2] Biological Dynamics of Forest Fragments Project, National Institute for Amazonian Research (INPA), C.P. 478, Manaus, AM 69011-970, Brazil

Summary

I summarize key findings from the Biological Dynamics of Forest Fragments Project, the world's largest and longest-running experimental study of habitat fragmentation. Although initially designed to assess the influence of fragment area on Amazonian biotas, the project has yielded insights that go far beyond the original scope of the study. Results suggest that edge effects play a key role in fragment dynamics, that the matrix has a major influence on fragment connectivity and functioning, and that many Amazonian species avoid even small (<100 m wide) clearings. The effects of fragmentation are highly eclectic, altering species richness and abundances, species invasions, forest dynamics, the trophic structure of communities, and a variety of ecological and ecosystem processes. Moreover, forest fragmentation appears to interact synergistically with ecological changes such as hunting, fires, and logging, collectively posing an even greater threat to the rainforest biota.

Keywords: Amazon, edge effects, forest dynamics, habitat fragmentation, hunting, logging, microhabitat changes, rainforest, surface fires.

1 Introduction

The Amazon basin contains over half of Earth's remaining tropical rainforests and is experiencing high rates of deforestation that have accelerated substantially over the past 15 years (Laurance et al. 2001a, 2004, INPE 2005). Because rapid forest conversion is causing widespread habitat fragmentation (Skole and Tucker 1993, Laurance 1998, 2005a), the fates of many Amazonian species will ultimately depend on their capacity to persist in fragmented landscapes or isolated nature reserves.

Tscharntke T, Leuschner C, Zeller M, Guhardja E, Bidin A (eds), The stability of tropical rainforest margins, linking ecological, economic and social constraints of land use and conservation, Springer Verlag Berlin 2007, pp 11-37

The Biological Dynamics of Forest Fragments Project (BDFFP) was initiated in 1979 as a large-scale experiment to assess the effects of fragmentation on Amazonian biotas (Lovejoy et al. 1983, 1986, Bierregaard et al. 1992, Laurance et al. 2002). It is the world's largest and longest-running experimental study of habitat fragmentation (cf. Debinski and Holt 2000). Originally, the project's main goals were to assess the influence of fragment size on Amazonian animal and plant communities, to identify a minimum critical size for rainforest reserves, and to help resolve the heated SLOSS (single large versus several small reserves) debate (e.g., Simberloff and Abele 1976, Wilcox and Murphy 1985). Over time, however, many additional research aims have been added as new insights have developed.

A key feature of the BDFFP is that standardized abundance data were collected for trees, understory birds, mammals, amphibians, and various invertebrate groups prior to experimental isolation of the forest fragments. This permitted a far more rigorous assessment of fragmentation effects than would have been possible using only comparisons of fragmented versus intact forest. In addition, the long-term nature of the BDFFP and its synthetic approach, integrating studies of many taxa and numerous ecological and ecosystem processes, have provided insights that are impossible in most other fragmentation studies.

Here I synthesize key BDFFP findings from the past 26 years, based on a survey of over 400 publications and theses, and I also highlight their implications for forest conservation. The first part of this review focuses on extrinsic factors that influence fragment biotas—particularly area, edge, matrix, isolation, and sample effects. The second part identifies key community- and ecosystem-level effects of fragmentation on tropical forests.

1.1 Study area

The 1000-km^2 study site is located 80 km north of Manaus, Brazil in central Amazonia (2^o 30$'$ S, 60^o W) at 50-100 m elevation (Figure 1). Local soils are nutrient-poor sandy or clay-rich ferrasols, which are widespread in the Amazon basin (Brown 1987). As is typical of the basin, the topography is relatively flat but dissected by many stream gullies. Rainfall ranges from 1,900-3,500 mm annually with a dry season from June to October (Laurance 2001). The climate regime is intermediate between that of the very wet western Amazon and drier, more-seasonal areas in the southeastern and north-central basin. The forest canopy is 30-37 m tall, with emergents reaching to 55 m. Species richness of trees is very high and can exceed 280 species ($\geq$10 cm diameter) per ha (Oliveira and Mori 1999).

The study area is surrounded by large expanses (>200 km) of continuous forest to the west, north, and east. In the early 1980s, five 1-ha fragments, four 10-ha fragments, and two 100-ha fragments were isolated by distances of 80-650 m from surrounding forest by clearing the intervening vegetation to establish cattle pastures. Fragments were fenced to prevent encroachment

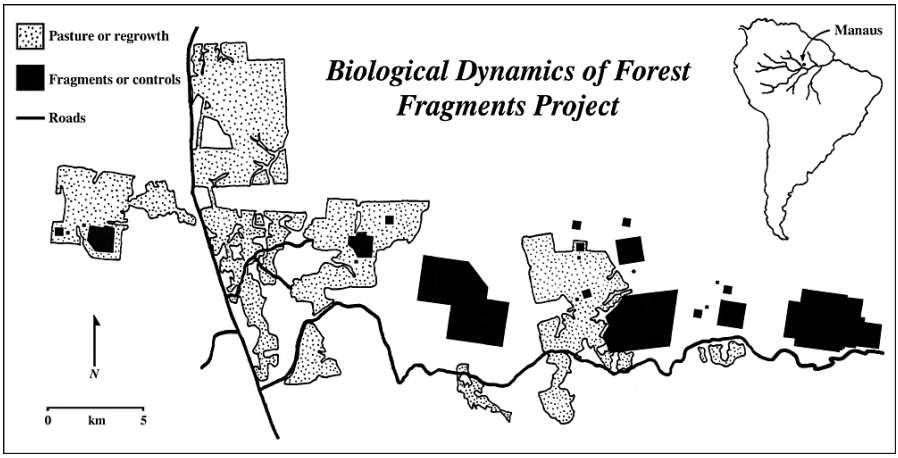

Fig. 1. The BDFFP study area in central Amazonia, showing locations of forest fragments and control sites in intact forest.

by cattle. Twelve reserves ranging from 1-1000 ha in area (three of 1-ha, four of 10 ha, two of 100 ha, and three of 1000 ha) were delineated in nearby continuous forest to serve as experimental controls. Because of low pasture productivity, the ranches were gradually abandoned, and 3-15 m tall secondary forests (dominated by *Cecropia* spp. or *Vismia* spp.) proliferated in many formerly cleared areas. To help maintain fragment isolation, 100 m-wide strips of regrowth were cleared and burned around each fragment on 2-3 occasions. Detailed descriptions of the study area, including the history of each fragment and its surrounding vegetation, are provided elsewhere (Lovejoy et al. 1986, Bierregaard and Stouffer 1997).

2 Extrinsic Factors Affecting Fragment Biotas

2.1 Sample effects

Forest fragments contain a limited subset of any regional biota, in part because small patches inevitably sample fewer species and less habitat diversity than do larger patches (e.g., Wilcox and Murphy 1985, Haila et al. 1993). Results from the BDFFP suggest that such sample effects could be especially important for Amazonian species, which often have patchy distributions at varying spatial scales and complex patterns of endemism (e.g., Zimmerman and Bierregaard 1986, Vasconcelos 1988, Allmon 1991, Rankin-de Merona et al. 1992, Souza and Brown 1994, Didham et al. 1998a, Laurance et al. 1998a, Peres 2005). Pronounced clumping means many species will be missing from any particular fragment or reserve simply because they never occurred there in the first place.

Another key factor is that, in tropical rainforests, most species are locally rare throughout all or much of their geographic range (Hubbell and Foster 1986, Pittman et al. 1999). The acidic, nutrient-poor soils prevalent in much of Amazonia (Brown 1987) appear to promote animal rarity by limiting fruit and flower production and reducing the nutrient content of foliage (reviewed in Laurance 2001). As a result, many invertebrates (Vasconcelos 1988, Becker et al. 1991) and vertebrates (Emmons 1984, Rylands and Keuroghlian 1988, Kalko 1998, Stouffer and Bierregaaard 1995a, Spironello 2001) are considerably less abundant in forests overlaying nutrient-poor Amazonian soils than they are in more-productive areas of the Neotropics. Intrinsic rarity is a critical feature, as demonstrated by studies of Amazonian trees. Even if a species is present when a fragment is initially isolated, its population may be so small that it has little chance of persisting in the long term (Laurance et al. 1998a).

2.2 Area effects

As is generally expected based on other investigations in the tropics (e.g. Laurance and Bierregaard 1997 and references therein, Harcourt and Doherty 2005), BDFFP researchers have often found that species richness is positively correlated with fragment size, and that intact forest contains more species per unit area than fragments (e.g. Figure 2). This arises because many large mammals (Lovejoy et al. 1986), primates (Rylands and Keuroghlian 1988, Schwartzkopf and Rylands 1989, Gilbert and Setz 2001), understory birds (Stouffer and Bierregaard 1995b, Stratford and Stouffer 1999, Ferraz et al. 2003), and even certain beetle, ant, bee, termite, and butterfly species (Powell and Powell 1987, Vasconcelos 1988, Klein 1989, Souza and Brown 1994, Brown and Hutchings 1997, Didham 1997a) are highly sensitive to fragment area. A number of these species have disappeared from even the largest (100 ha) fragments in the study area.

The prediction that extinction rates will be negatively correlated with fragment area (MacArthur and Wilson 1967) is also supported by the BDFFP results. Once isolated, small (1-10 ha) fragments initially lose species at a remarkably high rate; for example, dung and carrion beetle assemblages were markedly altered only 2-6 years after fragment isolation (Klein 1989). Local extinctions of birds (Harper 1989, Stouffer and Bierregaard 1995b, Stratford and Stouffer 1999), primates (Lovejoy et al. 1986, Schwartzkopf and Rylands 1989, Gilbert and Setz 2001), and butterflies (Brown and Hutchings 1997) have also occurred more rapidly in small (1-10 ha) than in large (100 ha) fragments.

In contrast, a few taxa have remained stable or even increased in species richness after fragment isolation. Frog richness increased because of an apparent resilience of most rainforest frogs to area and edge effects and an influx of non-rainforest species from the surrounding matrix (Gascon 1993, Tocher et al. 1997). Butterfly richness also rose after fragment isolation, largely from an invasion of generalist matrix species at the expense of forest-interior butterflies

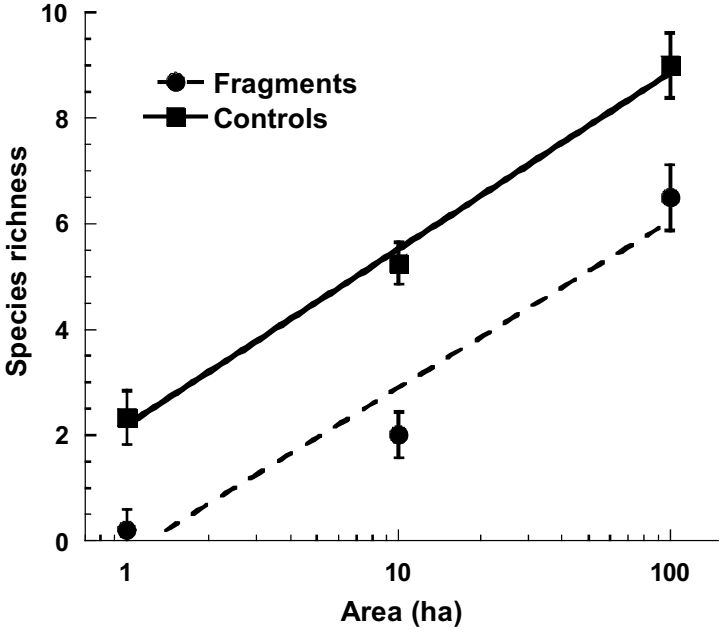

Fig. 2. Species-area relationships for nine species of terrestrial insectivorous birds (mean ± S.E.) in the BDFFP study area. Regression lines are fitted separately for fragments (R^2=94.3%) and control sites (R^2=99.4%) (after Stratford and Stouffer 1999).

(Brown and Hutchings 1997). Small mammal richness has not declined in the BDFFP fragments because most species readily use edge and regrowth habitats (Malcolm 1997). Collectively, BDFFP results reveal that the responses of different species and taxonomic groups to fragmentation are highly individualistic, and suggest that species with small area needs that tolerate matrix and edge habitats are the least vulnerable (e.g., Offerman et al. 1995, Stouffer and Bierregaard 1995b, Didham et al. 1998a, Gascon et al. 1999).

2.3 Edge effects

Edge effects can be a major structuring force in fragmented ecosystems (e.g. Laurance 1997, Didham 1997a, Ries et al. 2004). The BDFFP has helped to reveal the remarkable diversity of edge effects in fragmented rainforests, which alter physical gradients, species distributions, and many ecological and ecosystem processes (Figure 3). Microclimatic changes near edges, such as reduced humidity, increased light, and greater temperature variability, penetrate up to 60 m into fragment interiors (Kapos 1989) and can negatively affect species adapted for humid, dark forest interiors (Lovejoy et al. 1986, Benitez-Malvido 1998). Leaf litter accumulates near edges (Carvalho and Vasconcelos 1999,

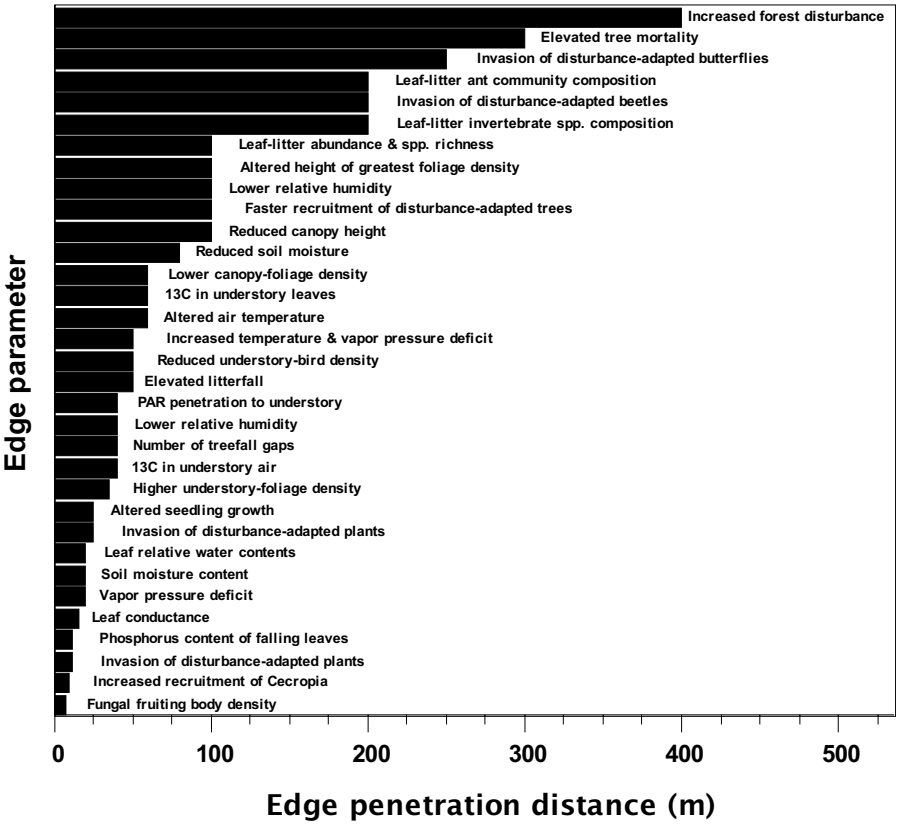

Fig. 3. Penetration distances of different edge effects into the BDFFP forest remnants.

Didham and Lawton 1999) because drought-stressed trees shed leaves and possibly because drier edge conditions slow litter decomposition (Kapos et al. 1993, Didham 1998, Vasconcelos and Laurance 2005). Accumulating litter may negatively affect seed germination (Bruna 1999) and seedling survival (Scariot 2001) and makes forest edges vulnerable to surface fires during droughts (Cochrane et al. 1999).

One of the most striking edge effects is a sharp increase in rates of tree mortality and damage (Ferreira and Laurance 1997, Laurance et al. 1998b). When an edge is created, some trees simply drop their leaves and die standing (Lovejoy et al. 1986), apparently because abrupt changes in light, temperature, or moisture exceed their physiological tolerances. Other trees are snapped or felled by winds, which accelerate over cleared land and then strike forest edges, creating strong turbulence (Laurance 1997). Finally, lianas (woody vines)—important structural parasites that reduce tree growth, survival, and

reproduction—increase markedly near edges and may further elevate tree mortality (Laurance et al. 2001b).

The abrupt rise in tree mortality fundamentally alters canopy-gap dynamics (Ferreira and Laurance 1997, Laurance et al. 1998b), which can influence forest structure, composition, and diversity (Brokaw 1985, Hubbell and Foster 1986, Denslow 1987). Smaller fragments often become hyper-disturbed, leading to progressive changes in floristic composition. New trees regenerating within 100 m of forest edges are significantly biased toward disturbance-loving pioneer and secondary species and against old-growth, forest-interior species (Laurance et al. 1998c, in press). The pioneer tree *Cecropia sciadophylla*, for example, has increased 33-fold in density since the BDFFP fragments were isolated (Laurance et al. 2001b).

Some animals respond positively to edges. Certain termites, leafhoppers, scale insects, aphids, aphid-tending ants (Fowler et al. 1993), and light-loving butterflies (Brown and Hutchings 1997) increase near edges. Birds that forage in treefall gaps, such as some arboreal insectivores, hummingbirds, and habitat generalists, often become abundant near edges (Bierregaard and Lovejoy 1989, Bierregaard 1990, Stouffer and Bierregaard 1995a, 1995b). Frugivorous bats increase near edges, probably because such areas have higher fruit abundance than forest interiors (Kalko 1998). The insectivorous marsupial *Metachirus nudicaudatus* apparently increased in fragments because dead trees and ground cover, which provide favored foraging microhabitats, increased near edges (Malcolm 1991).

Many other animal species respond negatively to edges and thus are likely to be vulnerable to fragmentation. Numerous flies, bees, wasps (Fowler et al. 1993), beetles (Didham et al. 1998a, 1998b), ants (Carvalho and Vasconcelos 1999), and butterflies (Brown and Hutchings 1997) decline in abundance near edges. A number of insectivorous understory birds avoid edges (Quintela 1985), particularly solitary species, obligatory ant followers, and those that forage in mixed-species flocks (S.G. Laurance 2004). Some frog species use breeding habitat independent of its proximity to edges (Gascon 1993), whereby others may be edge avoiders (e.g., Pearman 1997).

Edge effects in fragmented forests are evidently additive, whereby forest adjoined by two or more nearby edges suffers greater edge effects than does forest adjoined by just a single edge (Malcolm 1994, 1998, Ries et al. 2004, Fletcher 2005). In the BDFFP study area, an additive-edge model better predicts structural changes to forest fragments than does a single-edge model (Malcolm 1994). In addition, the population density of disturbance-adapted successional trees increased far more in edge plots with four nearby edges (658±850%) than in those with two (264±353%) or one (129±225%) nearby edges (nearby edges were defined as those within 100 m of the plot center). Species richness of successional trees and stand-level tree mortality were also much (ca. 50-120%) higher in plots with 2-4 nearby edges than in those with a single nearby edge (Laurance et al. 2006).

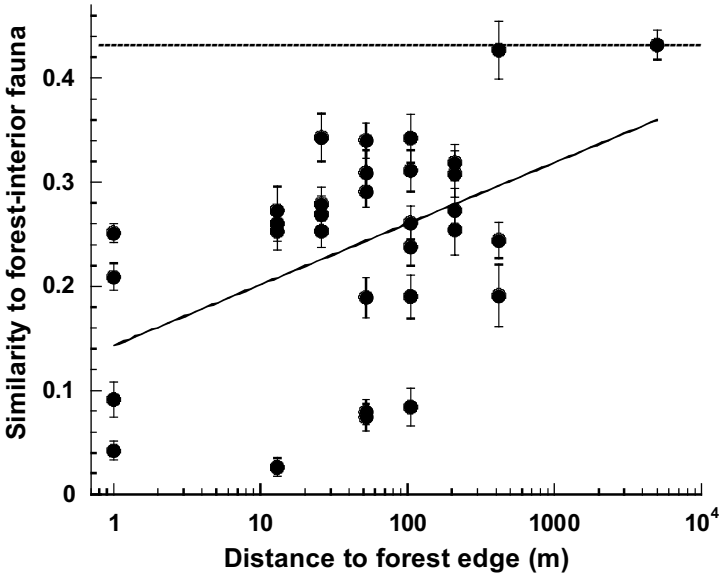

Fig. 4. Changes in the composition of leaf-litter beetle assemblages as a function of distance from forest edge. For each sample, the mean percentage similarity (± SE) to forest-interior samples (ca. 5000 m from edge) is shown. Dotted line shows the average background level of similarity among different forest-interior samples. The regression was highly significant (R^2=23.2%, p=0.005) (after Didham 1997b).

The most striking edge effects in the BDFFP study area occur within 100 m of forest edges (Figure 3). However, wind damage to forests can penetrate up to 300-400 m from edges (Laurance et al. 1998b, 2000, Lewis 1998), and changes in beetle, ant, and butterfly communities can be detected as far as 200-400 m from edges (Figure 4, Brown and Hutchings 1997, Didham 1997b, Carvalho and Vasconcelos 1999). Notably, some edge effects occur over even larger spatial scales in more-seasonal areas of the Amazon: ground fires in two fragmented landscapes of eastern Amazonia were sharply elevated in frequency within at least 2400 m of forest edges (Cochrane and Laurance 2002).

2.4 Edge evolution

Another important finding is that rapid changes in the physical permeability of edges occur in the initial years after fragmentation. Newly created edges are structurally open and thereby permeable to lateral light penetration and hot, dry winds from adjoining cattle pastures. After a few years, these microclimatic alterations decline in intensity as edges are partially sealed by a profusion of secondary growth (Kapos 1989, Camargo and Kapos 1995, Kapos et al. 1997). Desiccation-related plant mortality may also decline over time

because of an increase in drought-tolerant species or physiological acclimation of plants near edges. Unlike microclimatic changes, however, wind damage to forests is unlikely to lessen as fragment edges become older and less permeable because downwind turbulence usually increases as edge permeability is reduced (Savill 1983). In terms of edge permeability, three phases of edge evolution can be identified: initial isolation, edge-closure, and post-closure.

In the initial isolation phase (<1 year after edge formation), the gradient between the forest interior and edge is steepest, with hot, dry conditions and increased light and wind penetrating into the fragment. There is a dramatic pulse in tree mortality; many trees die standing (Laurance et al. 1998b). Leaf-litter accumulates as drought-stressed trees shed leaves to conserve water, or replace shade-adapted leaves with sun-adapted leaves (Didham 1998). Abundances of many animals fluctuate sharply. The most sensitive species decline almost immediately.

During the edge-closure phase (1-5 years after edge formation), a proliferation of secondary vegetation and lateral branching by edge trees progressively seals the edge. Edge gradients in microclimate become more complex but do not disappear entirely (Kapos et al. 1997). Plants near the edge die or become physiologically acclimated to edge conditions. Treefall gaps proliferate within the first 100-300 m of edges, partly as a result of increased windthrow. Additional animal species disappear from fragments. Edge-favoring plants and animals sometimes increase dramatically in abundance (Laurance and Bierregaard 1997).

In the post-closure phase (>5 years after edge formation), edge-related changes are largely stabilized, although external land-use changes (such as fires or the development of adjoining regrowth) can disrupt this equilibrium (Gascon et al. 2000). Windthrow remains elevated near edges, despite the fact that the edge is partially sealed by secondary growth. Proliferating lianas near edges probably contribute to increased tree mortality. Turnover rates of trees increase near edges because of elevated tree mortality and recruitment, and increasing numbers of short-lived pioneer species. Pioneer plants have rapid leaf replacement, contributing to the accumulation of leaf litter near edges. Although edge closure occurs relatively quickly in tropical rainforests because of rapid plant growth, edges are still more dynamic and vulnerable to climatic vicissitudes than are forest interiors (Laurance et al. 2002).

2.5 Matrix effects

An increasing body of evidence suggests that the matrix of modified land surrounding forest fragments can have manifold effects on fragment ecology (e.g. Gustafson and Gardner 1996, Weins 1997, Bender and Fahrig 2005). For example, fragments surrounded by 5-10 m-tall regrowth forest experienced less-intensive changes in microclimate (Didham and Lawton 1999) and had lower edge-related tree mortality (Mesquita et al. 1999) than did similar fragments adjoined by cattle pastures. Edge avoidance by mixed-species bird flocks was