



Review

The fate of Amazonian forest fragments: A 32-year investigation

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ABSTRACT

We synthesize findings to date from the world's largest and longest-running experimental study of habitat fragmentation, located in central Amazonia. Over the past 32 years, Amazonian forest fragments ranging from 1 to 100 ha have experienced a wide array of ecological changes. Edge effects have been a dominant driver of fragment dynamics, strongly affecting forest microclimate, tree mortality, carbon storage, fauna, and other aspects of fragment ecology. However, edge-effect intensity varies markedly in space and time, and is influenced by factors such as edge age, the number of nearby edges, and the adjoining matrix of modified vegetation surrounding fragments. In our study area, the matrix has changed markedly over the course of the study (evolving from large cattle pastures to mosaics of abandoned pasture and regrowth forest) and this in turn has strongly influenced fragment dynamics and faunal persistence. Rare weather events, especially windstorms and droughts, have further altered fragment ecology. In general, populations and communities of species in fragments are hyperdynamic relative to nearby intact forest. Some edge and fragment-isolation effects have declined with a partial recovery of secondary forests around fragments, but other changes, such as altered patterns of tree recruitment, are ongoing. Fragments are highly sensitive to external vicissitudes, and even small changes in local land-management practices may drive fragmented ecosystems in markedly different directions. The effects of fragmentation are likely to interact synergistically with other anthropogenic threats such as logging, hunting, and especially fire, creating an even greater peril for the Amazonian biota.

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1. Introduction

The rapid loss and fragmentation of old-growth forests are among the greatest threats to tropical biodiversity (Lovejoy et al., 1986; Sodhi et al., 2004; Laurance and Peres, 2006). More than half of all surviving tropical forest occurs in the Amazon Basin, which is being seriously altered by large-scale agriculture (Fearnside, 2001; Gibbs et al., 2010), industrial logging (Asner et al., 2005), proliferating roads (Laurance et al., 2001a; Killeen, 2007), and oil and gas developments (Finer et al., 2008).

The exploitation of Amazonia is driving forest fragmentation on a vast spatial scale. By the early 1990s, the area of Amazonian forest that was fragmented (<100 km²) or vulnerable to edge effects (<1 km from edge) was over 150% greater than the area that had been deforested (Skole and Tucker, 1993). From 1999 to 2002, deforestation and logging in Brazilian Amazonia respectively created ~32,000 and ~38,000 km of new forest edge annually (Broadbent et al., 2008). Prevailing land uses in Amazonia, such as cattle ranching and small-scale farming, produce landscapes dominated by small (<400 ha) and irregularly shaped forest fragments (Cochrane and Laurance, 2002; Broadbent et al., 2008). Such fragments are highly vulnerable to edge effects, fires, and other deleterious consequences of forest fragmentation (Laurance et al., 2002; Barlow et al., 2006; Cochrane and Laurance, 2008).

Starting in 1979, the Biological Dynamics of Forest Fragments Project (BDFFP) has been assessing the impacts of fragmentation on the Amazon rainforest and biota (Lovejoy et al., 1986; Bierregaard et al., 1992; Pimm, 1998; Laurance et al., 2002). Today, 32 years later, it is the world's largest and longest-running experimental study of

habitat fragmentation, as well as one of the most highly cited ecological investigations ever conducted (Gardner et al., 2009; Peres et al., 2010). As of October 2010, BDFFP researchers had produced 562 publications and 143 completed graduate theses (<http://pdfff.inpa.gov.br>), focusing on the responses of a wide array of animal and plant taxa to fragmentation as well as research on secondary forests, global-change phenomena, and basic forest ecology.

The last general review of forest fragmentation research at the BDFFP was nearly a decade ago (Laurance et al., 2002), and we present here an updated synthesis. We highlight several key conclusions from our last review but emphasize new findings and their implications for forest conservation, including recent works by BDFFP investigators that encompass large expanses of the Amazon basin.

2. Project background

The BDFFP is located 80 km north of Manaus, Brazil and spans ~1000 km² (Fig. 1). The topography is relatively flat (80–160 m elevation) but dissected by numerous stream gullies. The heavily weathered, nutrient-poor soils of the study area are typical of large expanses of the Amazon Basin. Rainfall ranges from 1900 to 3500 mm annually with a moderately strong dry season from June to October. The forest canopy is 30–37 m tall, with emergents to 55 m. Species richness of trees (≥ 10 cm diameter-at-breast-height) often exceeds 280 species ha⁻¹ (Oliveira and Mori, 1999; Laurance et al., 2010) with a comparably high level of diversity also evident in many other plant and animal taxa.

The study area includes three large cattle ranges (~5000 ha each) containing 11 forest fragments (five of 1 ha, four of 10 ha,

- Bruna, E.M., Vasconcelos, H.L., Heredia, S., 2005. The effect of habitat fragmentation on communities of mutualists: a test with Amazonian ants and their host plants. *Biol. Conserv.* 124, 209–216.
- Bührnheim, C.M., Fernandes, C.C., 2003. Structure of fish assemblages in Amazonian rainforest streams: effects of habitats and locality. *Copeia* 2003, 255–262.
- Camargo, J.L.C., Kapos, V., 1995. Complex edge effects on soil moisture and microclimate in central Amazonian forest. *J. Trop. Ecol.* 11, 205–211.
- Carvalho, K.S., Vasconcelos, H.L., 1999. Forest fragmentation in central Amazonia and its effects on litter-dwelling ants. *Biol. Conserv.* 91, 151–158.
- Chambers, J.Q., Higuchi, N., Schimel, J.P., 1998. Ancient trees in Amazonia. *Nature* 391, 135–136.
- Chazdon, R.L., Harvey, C.A., Komar, O., Griffith, D.M., Ferguson, B.G., Martinez-Ramos, M., Morales, H., Nigh, R., Soto-Pinto, L., van Breugel, M., Philpott, S.M., 2008. Beyond reserves: a research agenda for conserving biodiversity in human-modified tropical landscapes. *Biotropica* 41, 142–153.
- Cochrane, M.A., Laurance, W.F., 2002. Fire as a large-scale edge effect in Amazonian forests. *J. Trop. Ecol.* 18, 311–325.
- Cochrane, M.A., Laurance, W.F., 2008. Synergisms among fire, land use, and climate change in the Amazon. *Ambio* 37, 522–527.
- Cramer, J.M., Mesquita, R., Bentos, T., Moser, B., Williamson, G.B., 2007a. Forest fragmentation reduces seed dispersal of *Duckeodendron cestroides*, a Central Amazon endemic. *Biotropica* 39, 709–718.
- Cramer, J.M., Mesquita, R., Williamson, G.B., 2007b. Forest fragmentation differentially affects seed dispersal of large and small-seeded tropical trees. *Biol. Conserv.* 137, 415–423.
- D'Angelo, S., Andrade, A., Laurance, S.G., Laurance, W.F., Mesquita, R., 2004. Inferred causes of tree mortality in fragmented and intact Amazonian forests. *J. Trop. Ecol.* 20, 243–246.
- da Silva, J.M.C., Tabarelli, M., 2000. Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. *Nature* 404, 72–74.
- Develey, P., Stouffer, P.C., 2001. Roads affect movements by understory mixed-species flocks in central Amazonian Brazil. *Conserv. Biol.* 15, 1416–1422.
- Diamond, J.M., Bishop, K.D., Balen, S.V., 1987. Bird survival in an isolated Javan woodland: island or mirror? *Conserv. Biol.* 1, 132–142.
- Dick, C.W., 2001. Genetic rescue of remnant tropical trees by an alien pollinator. *Proc. Roy. Soc. B* 268, 2391–2396.
- Dick, C.W., Etchalecu, G., Austerlitz, F., 2003. Pollen dispersal of tropical trees (*Dinizia excelsa*; Fabaceae) by native insects and African honeybees in pristine and fragmented Amazonian rainforest. *Mol. Ecol.* 12, 753–764.
- Didham, R.K., Hammond, P.M., Lawton, J.H., Eggleton, P., Stork, N.E., 1998a. Beetle species responses to tropical forest fragmentation. *Ecol. Monogr.* 68, 295–303.
- Didham, R.K., Lawton, J.H., 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica* 31, 17–30.
- Didham, R.K., Lawton, J.H., Hammond, P.M., Eggleton, P., 1998b. Trophic structure stability and extinction dynamics of beetles (Coleoptera) in tropical forest fragments. *Proc. Roy. Soc. B* 353, 437–451.
- Fáveri, S.B., Vasconcelos, H.L., Dirzo, R., 2008. Effects of Amazonian forest fragmentation on the interaction between plants, insect herbivores, and their natural enemies. *J. Trop. Ecol.* 24, 57–64.
- Fearnside, P.M., 2001. Soybean cultivation as a threat to the environment in Brazil. *Environ. Conserv.* 28, 23–38.
- Fearnside, P.M., Graça, P.M.L.A., 2006. BR-319: Brazil's Manaus–Porto Velho highway and the potential impact of linking the arc of deforestation to central Amazonia. *Environ. Manage.* 38, 705–716.
- Ferraz, G., Nichols, J.D., Hines, J., Stouffer, P.C., Bierregaard, R.O., Lovejoy, T.E., 2007. A large-scale deforestation experiment: effects of patch area and isolation on Amazon birds. *Science* 315, 238–241.
- Ferraz, G., Russell, G.J., Stouffer, P.C., Bierregaard, R.O., Pimm, S.L., Lovejoy, T.E., 2003. Rates of species loss from Amazonian forest fragments. *Proc. Nat. Acad. Sci. USA* 100, 14069–14073.
- Finer, M., Jenkins, C., Pimm, S.L., Keane, B., Ross, C., 2008. Oil and gas projects in the western Amazon: threats to wilderness, biodiversity, and indigenous peoples. *PLoS ONE* 3, e2932.
- Fowler, H.G., Silva, C.A., Ventincinque, E., 1993. Size, taxonomic and biomass distributions of flying insects in central Amazonia: forest edge vs. Understory. *Rev. Biol. Trop.* 41, 755–760.
- Gardner, T.A., Barlow, J., Chazdon, R., Ewers, R., Harvey, C., Peres, C.A., Sodhi, N.S., 2009. Prospects for tropical forest biodiversity in a human-modified world. *Ecol. Lett.* 12, 561–582.
- Gascon, C., 1993. Breeding habitat use by Amazonian primary-forest frog species at the forest edge. *Biodiv. Conserv.* 2, 438–444.
- Gascon, C., Lovejoy, T.E., Bierregaard, R.O., Malcolm, J.R., Stouffer, P.C., Vasconcelos, H., Laurance, W.F., Zimmerman, B., Tocher, M., Borges, S., 1999. Matrix habitat and species persistence in tropical forest remnants. *Biol. Conserv.* 91, 223–229.
- Gibbs, H.K., Reusch, A.S., Achard, F., Clayton, M.K., Holmgren, P., Ramankutty, N., Foley, J.A., 2010. Tropical forests were the primary sources of new agricultural lands in the 1980s and 1990s. *Proc. Nat. Acad. Sci. USA* 107, 16732–16737.
- Gilbert, B., Laurance, W.F., Leigh, E.G., Nascimento, H., 2006. Can neutral theory predict the responses of Amazonian tree communities to forest fragmentation? *Am. Nat.* 168, 304–317.
- Gilbert, K.A., Setz, E.Z.F., 2001. Primates in a fragmented landscape: six species in central Amazonia. In: Laurance, W.F., Bierregaard, R.O. (Eds.), *Tropical Forest Remnants: Ecology, Management and Conservation of Fragmented Communities*. University of Chicago Press, Chicago, pp. 207–221.
- Girão, L.C., Lopes, A.V., Tabarelli, M., Bruna, E.M., 2007. Changes in tree reproductive traits reduce functional diversity in a fragmented Atlantic forest landscape. *PLoS ONE* 2, e908. doi:10.1371/journal.pone.0000908.
- Groeneveld, J., Alves, L., Bernacci, L., Catharino, E., Knogge, C., Metzger, J., Pütz, S., Huth, A., 2009. The impact of fragmentation and density regulation on forest succession in the Atlantic rain forest. *Ecol. Model.* 220, 2450–2459.
- Harper, L.H., 1989. The persistence of ant-following birds in small Amazonian forest fragments. *Acta Amazonica* 19, 249–263.
- Hubbell, S.P., 2001. *The Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, New Jersey.
- Janzen, D.H., 1983. No park is an island: Increase in interference from outside as park size increases. *Oikos* 41, 402–410.
- Jorge, M.L., 2008. Effects of forest fragmentation on two sister genera of Amazonian rodents (*Myoprocta acouchy* and *Dasyprocta leporina*). *Biol. Conserv.* 141, 617–623.
- Kapos, V., 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. *J. Trop. Ecol.* 5, 173–185.
- Killeen, T.J., 2007. *A Perfect Storm in the Amazon Wilderness: Development and Conservation in the Context of the Initiative for the Integration of the Regional Infrastructure of South America (IIRSA)*. Conservation International, Washington, DC.
- Klein, B.C., 1989. Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. *Ecology* 70, 1715–1725.
- Laurance, S.G., 2004. Responses of understory rain forest birds to road edges in central Amazonia. *Ecol. Appl.* 14, 1344–1357.
- Laurance, S.G., Gomez, M.S., 2005. Clearing width and movements of understory rainforest birds. *Biotropica* 37, 149–152.
- Laurance, S.G., Laurance, W.F., Andrade, A., Fearnside, P.M., Harms, K., Luizão, R., 2010. Influence of soils and topography on Amazonian tree diversity: a landscape-scale study. *J. Veg. Sci.* 21, 96–106.
- Laurance, S.G., Laurance, W.F., Nascimento, H., Andrade, A., Fearnside, P.M., Rebello, E., Condit, R., 2009a. Long-term variation in Amazon forest dynamics. *J. Veg. Sci.* 20, 323–333.
- Laurance, S.G., Stouffer, P.C., Laurance, W.F., 2004. Effects of road clearings on movement patterns of understory rainforest birds in central Amazonia. *Conserv. Biol.* 18, 1099–1109.
- Laurance, W.F., 1991. Ecological correlates of extinction proneness in Australian tropical rainforest mammals. *Conserv. Biol.* 5, 79–89.
- Laurance, W.F., 2001. The hyper-diverse flora of the central Amazon: an overview. In: Bierregaard, R.O., Gascon, C., Lovejoy, T.E., Mesquita, R. (Eds.), *Lessons from Amazonia: Ecology and Conservation of a Fragmented Forest*. Yale University Press, New Haven, Connecticut, pp. 47–53.
- Laurance, W.F., 2002. Hyperdynamism in fragmented habitats. *J. Veg. Sci.* 13, 595–602.
- Laurance, W.F., 2004. Forest-climate interactions in fragmented tropical landscapes. *Phil. Trans. Roy. Soc. B* 359, 345–352.
- Laurance, W.F., 2005. When bigger is better: the need for Amazonian megareserves. *Trends Ecol. Evol.* 20, 645–648.
- Laurance, W.F., 2007. Have we overstated the tropical biodiversity crisis? *Trends Ecol. Evol.* 22, 65–70.
- Laurance, W.F., 2008. Theory meets reality: how habitat fragmentation research has transcended island biogeographic theory. *Biol. Conserv.* 141, 1731–1744.
- Laurance, W.F., Bierregaard, R.O. (Eds.), 1997. *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*. University of Chicago Press, Chicago.
- Laurance, W.F., Cochrane, M.A., 2001. Synergistic effects in fragmented landscapes. *Conserv. Biol.* 15, 1488–1489.
- Laurance, W.F., Cochrane, M., Bergen, S., Fearnside, P.M., Delamonica, P., Barber, C., D'Angelo, S., Fernandes, T., 2001a. The future of the Brazilian Amazon. *Science* 291, 438–439.
- Laurance, W.F., Delamonica, P., Laurance, S.G., Vasconcelos, H.L., Lovejoy, T.E., 2000. Rainforest fragmentation kills big trees. *Nature* 404, 836.
- Laurance, W.F., Ferreira, L.V., Rankin-de Merona, J.M., Laurance, S.G., 1998a. Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology* 79, 2032–2040.
- Laurance, W.F., Ferreira, L.V., Rankin-de Merona, J.M., Laurance, S.G., Hutchings, R., Lovejoy, T.E., 1998b. Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. *Conserv. Biol.* 12, 460–464.
- Laurance, W.F., Goosem, M., Laurance, S.G., 2009b. Impacts of roads and linear clearings on tropical forests. *Trends Ecol. Evol.* 24, 659–669.
- Laurance, W.F., Laurance, S.G., Delamonica, P., 1998c. Tropical forest fragmentation and greenhouse gas emissions. *For. Ecol. Manage.* 110, 173–180.
- Laurance, W.F., Laurance, S.G., Ferreira, L.V., Rankin-de Merona, J., Gascon, C., Lovejoy, T.E., 1997. Biomass collapse in Amazonian forest fragments. *Science* 278, 1117–1118.
- Laurance, W.F., Lovejoy, T.E., Vasconcelos, H., Bruna, E., Didham, R., Stouffer, P., Gascon, C., Bierregaard, R., Laurance, S.G., Sampaio, E., 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conserv. Biol.* 16, 605–618.
- Laurance, W.F., Luizão, R.C.C., 2007. Driving a wedge into the Amazon. *Nature* 448, 409–410.
- Laurance, W.F., Nascimento, H., Laurance, S.G., Andrade, A., Ewers, R., Harms, K., Luizão, R., Ribeiro, J., 2007. Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. *PLoS ONE* 2, e1017. doi:10.1371/journal.pone.00001017.
- Laurance, W.F., Nascimento, H., Laurance, S.G., Andrade, A., Fearnside, P.M., Ribeiro, J., 2006a. Rain forest fragmentation and the proliferation of successional trees. *Ecology* 87, 469–482.

- Laurance, W.F., Nascimento, H., Laurance, S.G., Andrade, A., Ribeiro, J., Giraldo, J.P., Lovejoy, T.E., Condit, R., Chave, J., D'Angelo, S., 2006b. Rapid decay of tree-community composition in Amazonian forest fragments. *Proc. Nat. Acad. Sci. USA* 103, 19010–19014.
- Laurance, W.F., Nascimento, H., Laurance, S.G., Condit, R., D'Angelo, S., Andrade, A., 2004. Inferred longevity of Amazonian rainforest trees based on a long-term demographic study. *For. Ecol. Manage.* 190, 131–143.
- Laurance, W.F., Peres, C.A. (Eds.), 2006. Emerging Threats to Tropical Forests. University of Chicago Press, Chicago.
- Laurance, W.F., Perez-Salicerup, D., Delamonica, P., Fearnside, P.M., D'Angelo, S., Jerozolinski, A., Pohl, L., Lovejoy, T.E., 2001b. Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology* 82, 105–116.
- Laurance, W.F., Useche, D.C., 2009. Environmental synergisms and extinctions of tropical species. *Conserv. Biol.* 23, 1427–1437.
- Laurance, W.F., Williamson, G.B., 2001. Positive feedbacks among forest fragmentation, drought, and climate change in the Amazon. *Conserv. Biol.* 15, 1529–1535.
- Laurance, W.F., Williamson, G.B., Delamonica, P., Olivera, A., Gascon, C., Lovejoy, T.E., Pohl, L., 2001c. Effects of a strong drought on Amazonian forest fragments and edges. *J. Trop. Ecol.* 17, 771–785.
- Leidner, A.K., Haddad, N.M., Lovejoy, T.E., 2010. Does tropical forest fragmentation increase long-term variability of butterfly communities? *PLoS ONE* 5, e9534. doi:10.1371/journal.pone.0009534.
- Lima, M., Gascon, C., 1999. The conservation value of linear forest remnants in central Amazonia. *Biol. Conserv.* 91, 241–247.
- Lovejoy, T.E., Bierregaard, R.O., Rylands, A.B., Malcolm, J.R., Quintela, C., Harper, L., Brown, K., Powell, A., Powell, G., Schubart, H., Hays, M., 1986. Edge and other effects of isolation on Amazon forest fragments. In: Soulé, M.E. (Ed.), *Conservation Biology: The Science of Scarcity and Diversity*. Sinauer, Sunderland, Massachusetts, pp. 257–285.
- Lovejoy, T.E., Oren, D.C., 1981. Minimum critical size of ecosystems. In: Burgess, R.L., Sharp, D.M. (Eds.), *Forest Island Dynamics in Man-dominated Landscapes*. Springer-Verlag, New York, pp. 7–12.
- Lovejoy, T.E., Rankin, J.M., Bierregaard, R.O., Brown, K.S., Emmons, L.H., Van der Voort, M.E., 1984. Ecosystem decay of Amazon forest fragments. In: Nitecki, M.H. (Ed.), *Extinctions*. University of Chicago Press, Chicago, pp. 295–325.
- Malcolm, J.R., 1994. Edge effects in central Amazonian forest fragments. *Ecology* 75, 2438–2445.
- Malcolm, J.R., 1997. Biomass and diversity of small mammals in Amazonian forest fragments. In: Laurance, W.F., Bierregaard, R.O. (Eds.), *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*. University of Chicago Press, Chicago, pp. 207–221.
- Malcolm, J.R., 1998. A model of conductive heat flow in forest edges and fragmented landscapes. *Clim. Change* 39, 487–502.
- Mesquita, R., Delamônica, P., Laurance, W.F., 1999. Effects of surrounding vegetation on edge-related tree mortality in Amazonian forest fragments. *Biol. Conserv.* 91, 129–134.
- Mesquita, R., Ickes, K., Ganade, G., Williamson, G.B., 2001. Alternative successional pathways in the Amazon basin. *J. Ecol.* 89, 528–537.
- Mestre, L.A.M., Gasnier, T.R., 2008. Populações de aranhas errantes do gênero *Ctenus* em fragmentos florestais na Amazônia Central. *Acta Amazonica* 38, 159–164.
- Michalski, F., Peres, C.A., 2005. Anthropogenic determinants of primate and carnivore local extinctions in a fragmented forest landscape of Southern Amazonia. *Biol. Conserv.* 124, 383–396.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858.
- Nascimento, H., Andrade, A., Camargo, J., Laurance, W.F., Laurance, S.G., Ribeiro, J., 2006. Effects of the surrounding matrix on tree recruitment in Amazonian forest fragments. *Conserv. Biol.* 20, 853–860.
- Nascimento, H., Laurance, W.F., 2004. Biomass dynamics in Amazonian forest fragments. *Ecol. Appl.* 14, S127–S138.
- Neckel-Oliveira, S., Gascon, C., 2006. Abundance, body size and movement patterns of a tropical treefrog in continuous and fragmented forests of the Brazilian Amazon. *Biol. Conserv.* 128, 308–315.
- Nessimian, J.L., Venticinque, E.M., Zuanon, J., De Marco, P., Gordo, M., Fidelis, L., Batista, J., Juen, L., 2008. Land use, habitat integrity, and aquatic insect assemblages in central Amazonian streams. *Hydrobiologia* 614, 117–131.
- Norden, N., Mesquita, R., Bentos, T., Chazdon, R., Williamson, G.B., 2010. Contrasting community compensatory trends in alternative successional pathways in central Amazonia. *Oikos*. doi:10.1111/j.1600-0706.2010.18335.x.
- Oliveira de A.A., Mori, S.A., 1999. A central Amazonian terra firme forest. I. High tree species richness on poor soils. *Biodiv. Conserv.* 8, 1219–1244.
- Peres, C.A., 2005. Why we need megareserves in Amazonia. *Conserv. Biol.* 19, 728–733.
- Peres, C.A., Gardner, T.A., Barlow, J., Zuanon, J., Michalski, F., Lees, A., Vieira, I., Moreira, F., Feeley, K.J., 2010. Biodiversity conservation in human-modified Amazonian forest landscapes. *Biol. Conserv.* 143, 2314–2327.
- Pimm, S.L., 1998. The forest fragment classic. *Nature* 393, 23–24.
- Pimm, S.L., Jenkins, C., 2005. Sustaining the variety of life. *Sci. Am.* September, 66–73.
- Powell, A.H., Powell, G.V.N., 1987. Population dynamics of male euglossine bees in Amazonian forest fragments. *Biotropica* 19, 176–179.
- Quintela, C.E., 1985. Forest Fragmentation and Differential Use of Natural and Man-made Edges by Understory Birds in Central Amazonia. M.Sc. Thesis, University of Illinois, Chicago.
- Quintero, I., Roslin, T., 2005. Rapid recovery of dung beetle communities following habitat fragmentation in Central Amazonia. *Ecology* 86, 3303–3311.
- Radtke, M.G., da Fonseca, C., Williamson, G.B., 2008. Forest fragment size effects on dung beetle communities. *Biol. Conserv.* 141, 613–614.
- Rego, F., Venticinque, E.M., Brescovit, A., 2007. Effects of forest fragmentation on four *Ctenus* spider populations (Araneae, Ctenidae) in central Amazonia, Brazil. *Stud. Neotrop. Fauna Environ.* 42, 137–144.
- Ribeiro, M.B.N., Bruna, E.M., Mantovani, W., 2009. Influence of post-clearing treatment on the recovery of herbaceous plant communities in Amazonian secondary forests. *Restor. Ecol.* 18, 50–58.
- Sampaio, E.M., 2000. Effects of Forest Fragmentation on the Diversity and Abundance Patterns of Central Amazonian Bats. Ph.D. Dissertation, University of Tübingen, Berlin, Germany.
- Sampaio, E.M., Kalko, E., Bernard, E., Rodriguez-Herrera, B., Handley, C., 2003. A biodiversity assessment of bats (Chiroptera) in a tropical lowland forest of central Amazonia, including methodological and conservation considerations. *Stud. Neotrop. Fauna Environ.* 28, 17–31.
- Santos, B.A., Arroyo-Rodríguez, V., Moreno, C.E., Tabarelli, M., 2010. Edge-related loss of tree phylogenetic diversity in the severely fragmented Brazilian Atlantic forest. *PLoS ONE* 5, e12625. doi:10.1371/journal.pone.0012625.
- Scariot, A., 1999. Forest fragmentation effects on diversity of the palm community in central Amazonia. *J. Ecol.* 87, 66–76.
- Scariot, A., 2001. Weedy and secondary palm species in central Amazonian forest fragments. *Rev. Bot. Brasil.* 15, 271–280.
- Sizer, N., Tanner, E.V.J., 1999. Responses of woody plant seedlings to edge formation in a lowland tropical rainforest. *Amazonia. Biol. Conserv.* 91, 135–142.
- Sizer, N., Tanner, E.V.J., Kossman-Ferraz, I., 2000. Edge effects on litterfall mass and nutrient concentrations in forest fragments in central Amazonia. *J. Trop. Ecol.* 16, 853–863.
- Skole, D.S., Tucker, C.J., 1993. Tropical deforestation and habitat fragmentation in the Amazon: satellite data from 1978 to 1988. *Science* 260, 1905–1910.
- Sodhi, N.S., Koh, L.P., Brook, B.W., Ng, P., 2004. Southeast Asian biodiversity: an impending disaster. *Trends Ecol. Evol.* 19, 654–660.
- Stouffer, P.C., Bierregaard, R.O., 1995a. Effects of forest fragmentation on understory hummingbirds in Amazonian Brazil. *Conserv. Biol.* 9, 1085–1094.
- Stouffer, P.C., Bierregaard, R.O., 1995b. Use of Amazonian forest fragments by understory insectivorous birds. *Ecology* 76, 2429–2445.
- Stouffer, P.C., Bierregaard, R.O., Strong, C., Lovejoy, T.E., 2006. Long-term landscape change and bird abundance in Amazonian rainforest fragments. *Conserv. Biol.* 20, 1212–1223.
- Stouffer, P.C., Strong, C., Naka, L.N., 2008. Twenty years of understory bird extinctions from Amazonian rain forest fragments: consistent trends and landscape-mediated dynamics. *Divers. Distrib.* 15, 88–97.
- Stratford, J.A., Stouffer, P.C., 1999. Local extinctions of terrestrial insectivorous birds in Amazonian forest fragments. *Conserv. Biol.* 13, 1416–1423.
- Terborgh, J., Lopez, L., Nuñez, V.P., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G., Lambert, T., Balbas, L., 2001. Ecological meltdown in predator-free forest fragments. *Science* 294, 1923–1926.
- Timo, T.P.C., 2003. Influência de fragmentação e matriz sobre a comunidade de mamíferos de médio e grande porte em uma floresta de terra firme na Amazônia central. M.Sc. Thesis, National Institute for Amazonian Research (INPA), Manaus, Brazil.
- Tocher, M., Gascon, C., Zimmerman, B.L., 1997. Fragmentation effects on a central Amazonian frog community: a ten-year study. In: Laurance, W.F., Bierregaard, R.O. (Eds.), *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*. University of Chicago Press, Chicago, pp. 124–137.
- Trancoso, R., 2008. Hydrological Impacts of Deforestation in Small Catchments in Brazilian Amazonia. M.Sc. Thesis, National Institute for Amazonian Research (INPA), Manaus, Brazil.
- Uriarte, M., Bruna, E.M., Rubim, P., Anciäes, M., Jonckheere, I., 2010. Effects of forest fragmentation on the seedling recruitment of a tropical herb: assessing seed vs. safe-site limitation. *Ecology* 91, 1317–1328.
- Van Houtan, K.S., Pimm, S.L., Bierregaard, R.O., Lovejoy, T.E., Stouffer, P.C., 2006. Local extinctions in Amazonian forest fragments. *Evol. Ecol. Res.* 8, 129–148.
- Van Houtan, K.S., Pimm, S.L., Halley, J., Bierregaard, R.O., Lovejoy, T.E., 2007. Dispersal of Amazonian birds in continuous and fragmented forest. *Ecol. Lett.* 10, 219–229.
- Vasconcelos, H.L., Luizão, F.J., 2004. Litter production and litter nutrient concentrations in a fragmented Amazonian landscape: edge and soil effects. *Ecol. Appl.* 14, 884–892.
- Wilcox, B.A., Murphy, D.D., 1985. Conservation strategy: the effects of fragmentation on extinction. *Am. Nat.* 125, 879–887.
- Williamson, G.B., Laurance, W.F., Oliveira, A., Delamonica, P., Gascon, C., Lovejoy, T.E., Pohl, L., 2000. Amazonian wet forest resistance to the 1997–98 El Niño drought. *Conserv. Biol.* 14, 1538–1542.
- Williamson, G.B., Mesquita, R., 2001. Effects of fire on rain forest regeneration in the Amazon Basin. In: Laurance, W.F., Bierregaard, R.O. (Eds.), *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*. University of Chicago Press, Chicago, pp. 325–334.
- Zartman, C.E., 2003. Forest fragmentation effects on epiphyllous bryophyte communities in central Amazonia. *Ecology* 84, 948–954.
- Zartman, C.E., Nascimento, H.E.M., 2006. Are patch-tracking metacommunities dispersal limited? Inferences from abundance-occupancy patterns of epiphylls in Amazonian forest fragments. *Biol. Conserv.* 127, 46–54.
- Zartman, C.E., Shaw, A.J., 2006. Metapopulation extinction thresholds in rainforest remnants. *Am. Nat.* 167, 177–189.