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Forest fragmentation, synergisms and the impoverishment of neotropical forests

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Abstract. It is well documented that the negative effects of habitat fragmentation are strong enough to promote local as well as regional extinction of canopy and emergent trees in neotropical forests. However, forest fragmentation does not occur alone, but is always associated with other human-induced threats to trees, such as logging, forest burning and hunting of key vertebrate seed dispersers within forest remnants. This association occurs because forest resources are, at least during a certain period, the main income source for local human populations. It is now possible to establish how these threats act in concert causing tree species impoverishment. Based on a predictive model, it is predicted that the most fragmented forest regions have lost or will lose an important part of their tree diversity. New integrated research must urgently test this prediction and investigate how human activities might be regulated in both old and new tropical forest frontiers to avoid species loss. If we fail to do this we will miss the opportunity of proposing sound and efficient guidelines to rescue neotropical forests from species impoverishment.

Introduction

Laurance et al. (1998, 2000) have unequivocally demonstrated the negative impacts of habitat fragmentation on the abundance of neotropical trees in remnants of Amazonian rainforest. The major source of these impacts is edge effects – the diverse physical and biotic changes associated with the abrupt, artificial margins of forest fragments (Bierregaard et al. 2001). Most of their data come from the periodical resampling of a network of 69 permanent 1-ha plots set in nine fragments (1–100 ha) and at several comparable sites in intact forest. Plots were established and trees first sampled before fragment isolation, and since then plots have been protected from other human-caused disturbances such as logging and forest burning (Laurance et al. 2000). In a recent synthesis, Laurance (2001) argued that in fragments of Amazonian forest, tree species richness may substantially decline due to loss of disturbance-sensitive species, such as old-growth canopy/emergent trees. Because of this, forest fragments may support only an impoverished subset of trees from the original biota. Although the negative effects of forest fragmentation on seedling recruitment and sapling/adult survivorship appear to be strong enough to promote local (fragment) as well as regional (a set of fragments) tree extinctions, there is sufficient evidence in the literature that fragmentation does not occur alone, but that it is regularly and positively associated with other events (see Laurance and Cochrane 2001), which when acting in concert with habitat fragmentation will amplify the threats to trees in neotropical forests.

Forest fragmentation and threats to neotropical trees

In both old and new human-colonisation frontiers in the neotropical region, such as Amazonia and the Atlantic Forest, forest fragmentation is always associated with short- or long-term human establishment, and the ever-increasing commercial and subsistence needs for forest resources (e.g. timber, charcoal, firewood, game animals, fibres, nuts; Coimbra-Filho and Câmara 1996; Cullen et al. 2000; Carvalho et al. 2001; Laurance et al. 2001a; Peres 2001a). In these regions, habitat fragmentation usually provides better accessibility to forest resources and thus facilitates hunting (Chiarello 1999; Robinson et al. 1999; Silva and Tabarelli 2000; Peres 2001b), subsistence and industrial logging (Nepstad et al. 1999; Laurance 2000) and plant harvesting (Clark et al. 1995). Industrial logging operations in turn enhance forest fragmentation by desiccating forests through roads and tracks (Uhl et al. 1997; Veríssimo et al. 1995, 1998; Laurance 2000). Moreover, logging reduces canopy coverage and produces large amounts of organic debris. This fuel material, combined with litter and dead biomass produced by fragmentation itself, make fragments more susceptible to human-induced forest burning (Cochrane et al. 1999; Nepstad et al. 1999), that is, through fire originated in cattle pasture, slash-and-burn plots and commercial crops that surround fragments (Holdsworth and Uhl 1997; Gascon et al. 2000).

Associated with each one of these threats are ecological processes that have the potential to sharply reduce the population size of several tree species. Forest fragmentation and its edge effects (1) reduce plant recruitment due to habitat desiccation and seedling damage caused by litterfall and treefall near forest edges (Benítez-Malvido 1998; Bruna 1999; Didham and Lawton 1999; Tabarelli et al. 1999; Laurance 2001); (2) increase sapling mortality by competition with lianas, vines and ruderal species; and (3) increase adult mortality by elevated rates of uprooting and breakage near forest edges (Laurance et al. 1998, 2000, 2001b). Logging decreases the number of saplings by physical damage as well as the number of adult trees caused by over-harvesting (Uhl et al. 1997; Veríssimo et al. 1995, 1998; Nepstad et al. 1999). Forest burning depletes the soil seed bank (Cochrane and Schulze 1999) and increases rates of seedling/sapling/adult mortality due to burning and to competition with lianas, vines and ruderal species (Kauffman 1991; Holdsworth and Uhl 1997; Viana et al. 1997; Gascon et al. 2000; Pérez-Salicrup 2001). Hunting and/or habitat loss eliminate key vertebrate seed dispersers and consequently may decrease seedling recruitment by failure of seed germination (Asquith et al. 1999; Laurance 2001; Silva and Tabarelli 2000, 2001). Several neotropical tree species are currently threatened by one or a combination of the ecological processes described above. Martini et al. (1994) analysed a set of 305 Amazonian timber species and identified 41 canopy and emergent trees, which are susceptible to suffer local and regional population reduction due to logging pressures; among the most vulnerable trees are those with low ability to regenerate in human-disturbed areas. Uhl et al. (1997) and Nepstad et al. (1999) predicted a large-scale tree impoverishment of the Amazonian forest caused by undisciplined logging, forest burning and their consequences for sapling/adult mortality. Silva and Tabarelli (2000) predicted regional extinction of trees with large fruits due to failure of seedling recruitment and recolonisation by plants of remnants of the Atlantic forest in northeastern Brazil. Such failure is associated with lack of seed dispersal caused by the regional extinction of key vertebrate seed dispersers (e.g. primates and large-gaped birds) due to hunting and habitat loss. In the entire Brazilian Atlantic Forest, several canopy and emergent large trees are officially threatened with global extinction by both historical logging and habitat loss according to IUCN Red Lists (Tabarelli et al. 2002; M. Tabarelli, unpublished). Finally, under certain conditions in Amazonia and Brazilian Atlantic Forest, the synergisms among forest fragmentation, logging and forest burning are expected to extirpate not only tree species, but also entire fragments (Nepstad et al. 1999; Gascon et al. 2000; Cochrane and Laurance 2002).

A synthetic model describing threats and their synergisms

It is possible with the available information to establish how threats and ecological processes act in concert causing tree population decline (Figure 1). Fragmentation, logging and edge effects change forest structure and aboveground biomass (flow 1). Consequently, ruderal species invade fragments and the abundance of lianas and vines increases (flow 2). These changes in forest structure and composition make fragments prone to burning, especially in drier areas (flow 3). Periodic fires reduce canopy cover, drastically change vegetation structure along forest edges, sharply increase the density of vines, lianas and ruderal species, and consequently enhance the likelihood of new fires (flow 4). Parallel to all these events, key vertebrate seed dispersers are extirpated by hunting and/or habitat loss (flow 5). Through one or more of these flows, or by isolated impacts caused by logging and edge effects (flows 6 and 7), seedling recruitment declines and sapling/adult mortality increases among sensitive species. As a result, tree populations face both local and regional extinction (flow 8). Finally, there is a feedback loop (flow 9) to this model. Once local extinctions of tree species occur in fragments, this will lead to cascading effects on pollinators, seed predators, and seed dispersers of these tree species which, depending on their host specificity, will also be extirpated from these forest fragments. Such cascading effects of tree, insect and vertebrate species have the potential to seriously disrupt many basic ecological processes over larger areas, such as collapses in pollination, or higher level predator–prey interactions, further exacerbating fragmentation effects.

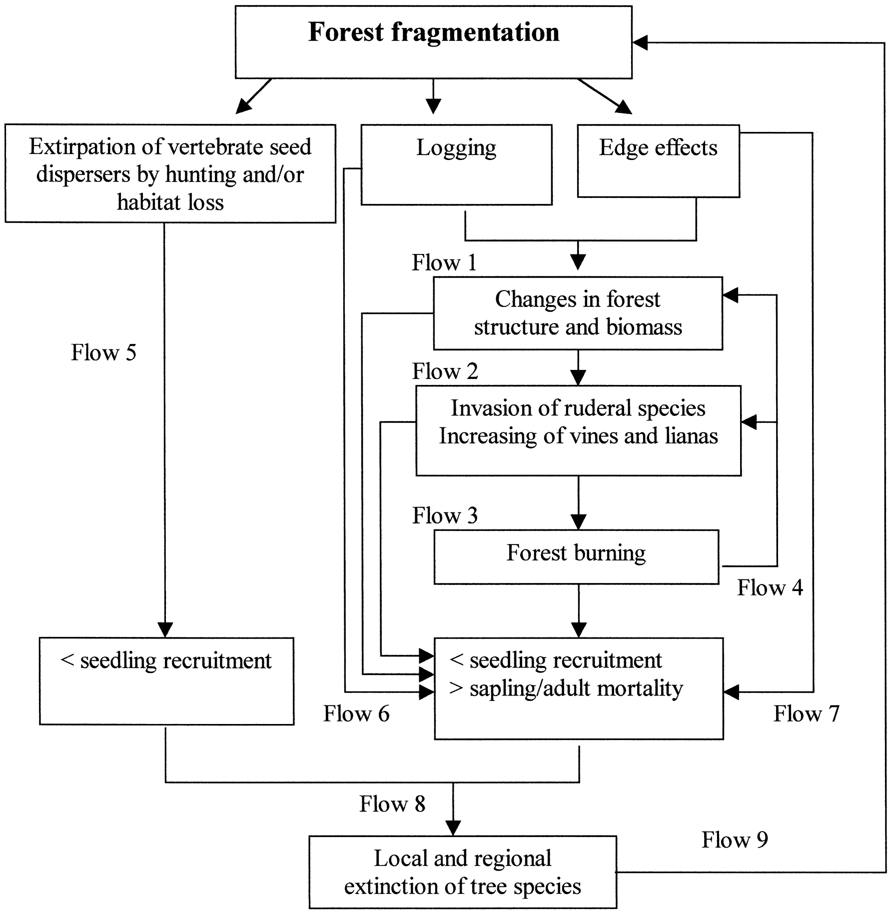

Figure 1. Forest fragmentation and its relationships with other threats and ecological processes that lead to local and regional extinction of tree populations (adapted from Tabarelli et al. 2002).

Although this synthetic model is a simple combination of threats described in the literature, it supports new and important predictions regarding biodiversity conservation. First, a large proportion of fragmented neotropical forest landscapes has faced or will face local and regional extinction of tree species (i.e. species impoverishment) by a combination of several threats that are catalysed by habitat fragmentation. Second, the magnitude of species loss depends on both the severity and extent of threats that are simultaneously imposed on fragments. Third, the most threatened trees are those that combine high timber value, vertebrate-dependence for seed dispersal and high sensitivity to edge effects, fire or competition with lianas, vines or ruderal species. Fourth, protection of neotropical forests from species impoverishment relies on the establishment of a set of conservation guidelines able to control the isolated or synergetic effects of these particular threats.

Concluding remarks

Our predictions do not invalidate the predictions of species loss and conservation guidelines derived from single-threat analysis, such as forest fragmentation (see Bierregaard et al. (2001) for a synthesis), but we call attention to the real magnitude of synergistic threats that some portions of neotropical forests have faced or will face. For instance, the human population size in Amazonia may double in the next two decades because of a new wave of immigrants (Laurance et al. 2001a; Peres 2001a). This increment is expected to drastically increase both the rate of habitat fragmentation and the current rate of 10 000–15 000 km^2 $year^{-1}$ of undisturbed forest severely degraded by logging (Nepstad et al. 1999; Laurance et al. 2001a). Thus, new integrated research must urgently (1) validate, refute or improve our model and its predictions; and (2) propose strategies to regulate the impact of human activities at old and new colonisation frontiers to reduce species loss. Similar to the Brazilian Atlantic Forest, other neotropical forests tend to be reduced to archipelagos of small fragments. Moreover, they will be completely incorporated in the living space of modern human societies and their needs for forest resources in the near future. If we fail to manage this incorporation for conservation, we will also fail to rescue neotropical forests from species impoverishment.

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