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SHORT COMMUNICATION

The effects of forest fragmentation and increased edge exposure on leaf litter accumulation

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In forested ecosystems leaf litter is generally the primary pathway through which nutrients are cycled from the canopy to the forest floor (other pathways include throughfall, stemflow and animal faeces; Jordan 1985). Consequently, any disturbance that alters the quantity or quality of litter can have dramatic impacts on nutrient cycling and the availability of essential nutrients to plants (Vitousek 1984). Fragmentation of tropical forests has been demonstrated to cause several changes in both the biotic (Cosson *et al.* 1999, Laurance *et al.* 1998, Saunders *et al.* 1991) and abiotic environments (Camargo & Kapos 1995, Debinski & Holt 2000, Laurance 2002, Laurance *et al.* 2002) and thus may influence litter accumulation in the remnant patches (Carvalho & Vasconcelos 1999, Didham 1998, Laurance *et al.* 2002).

In this study, I investigated the impact of habitat fragmentation on leaf litter accumulation by analysing differences in indices of litter depth across a set of land-bridge islands located in Lake Guri, Venezuela. Lake Guri is a large hydroelectric reservoir that was created in 1986 following the construction of the Raul Leoni Dam along the lower portion of the Rio Caroni in east-central Venezuela. The inundation of over 4300 km^2 of hilly terrain resulted in the fragmentation of once continuous forest into thousands of isolated islands (Morales & Gorzula 1986).

This study was conducted on a set of 18 small islands (0.2–4.0 ha, mean = 1.0 ha) located in the central portion of the lake. All study islands are isolated from any other landmass by at least 50 m and from the mainland by at least 350 m. The islands are all relatively close together (the greatest distance between any two islands is 17 km) and thus the islands were presumed to experience approximately the same weather conditions (mean annual temperature of 27.5 °C; mean annual rainfall of approximately 1500 mm, with the majority of precipitation occurring between the months of May and October; Alvarez *et al.* 1986). The habitats of all islands used in this study are classified as semi-deciduous tropical dry forest (Huber 1986, Terborgh *et al.* 1997). Canopy height ranges 15–20 m with occasional emergents reaching heights of up to 25 m. Further information on the structure and composition of the forests of Lake Guri can be found in Huber (1986) and Terborgh *et al.* (1997).

In order to determine the effects of habitat fragmentation and increased edge exposure on litter accumulation, I compared the relationship between litter depth and relative edge length (RE = perimeter/area). Small or convoluted islands have greater relative edge lengths compared with larger, rounder islands and thus are hypothesized to be more susceptible to edge effects (Saunders *et al.* 1991). In addition, I specifically investigated the potential for increased wind exposure along edges to affect litter accumulation by comparing litter depth on the windward (exposed) vs. leeward (protected) sides of islands. At Lake Guri, prevailing trade winds blow consistently from the east (Feeley *unpublished*). Accordingly, the predominantly east-facing sides of each island were designated as windward and the predominantly west-facing sides were designated as leeward.

I measured leaf litter depth in June 2001 and again in June 2002. During each year, all measurements were taken during a 2-wk period in order to minimize possible differences due to decomposition or litterfall between visits to islands (islands were sampled in random order). I measured leaf litter depth by inserting a wire probe through the accumulated litter into the soil surface and counting the number of leaf surfaces intercepted. This method does not provide an absolute measure of litter depth but rather is a measure of the leaf litter surface

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area per unit of surface area of the forest floor and will henceforth be referred to as the Leaf Litter Area Index (LLAI; analogous to Leaf Area Index). I used LLAI rather than direct measurements of litterfall because this measure determines the amount of accumulated litter available for decomposition and nutrient release after secondary dispersal by wind, animals or other agents.

LLAI was measured at 20 locations per side (windward and leeward) of each island (for a total of 40 measurements per island). Measurements were taken at arbitrary locations; the only criterion being that sample locations were separated by at least 5 m in order to minimize spatial autocorrelations. The Leaf Litter Area Index across all study islands ranged 0–14 and had a mean value of 1.77 ± 1.62 ($\pm$ SD). LLAI did not vary significantly between years (Repeated-measures ANOVA, $F = 0.008$, $P > 0.1$) and thus all analyses were conducted using combined data from both years of study. Mean LLAI was calculated for each island side and for each island as a whole.

The effects of edge length on litter accumulation were determined by regressing the LLAI of each island against RE. The potential effect of increased wind exposure was then investigated by comparing the relationship of LLAI to RE for windward vs. leeward sides of the islands. At the whole island scale, there was a strong negative relationship between LLAI and RE, such that islands with long relative edge lengths tended to have less accumulated leaf litter than islands with shorter relative edges ($LLAI_{island} = -0.0018RE + 2.6$, $R^2 = 0.33$, $P < 0.05$, Figure 1a). When only the leeward sides of the islands were included in the analysis, there was not a significant relationship between LLAI and RE ($LLAI_{lee} = -0.0016RE + 2.8$, $R^2 = 0.17$, $P > 0.05$, Figure 1b). In contrast, RE explains a high proportion of the variation in LLAI on the windward sides of islands ($LLAI_{wind} = -0.002RE + 2.45$, $R^2 = 0.47$, $P < 0.005$, Figure 1c).

I compared the LLAI on the island sides by using a paired t-test analysis and a two-factor ANOVA with island and side as the explanatory variables. In general, LLAI was higher on the leeward sides of islands than on the windward sides (paired t-test, $P < 0.005$, mean difference $= 0.56$, Figure 2), even after accounting for differences between islands (Two-Factor ANOVA: $F = 84.3$, $P < 0.0000$).

Some of the most dramatic effects caused by the fragmentation of tropical forests are associated with increased edge exposure (Laurance *et al.* 2002). In this study, I demonstrated that there is a significant negative relationship between a patch's relative edge length and leaf litter depth. This relationship may be attributed to increased wind exposure and penetration. At Lake Guri, strong winds blow uninterrupted across the lake and through the islands, in the process carrying fine litter material from the windward sides and depositing it on the more protected leeward sides (*personal observation*). This process leads to deeper litter accumulation on the protected sides than the exposed sides of islands. This hypothesis is supported by both the comparisons of litter depth between island sides and the strong negative relationship between litter depth and relative edge length on the windward sides of islands. The relationship between mean (whole-island) litter depth and edge length may be due to the fact that on small islands, such as those examined in this study, strong winds may actually carry some material completely off of the islands.

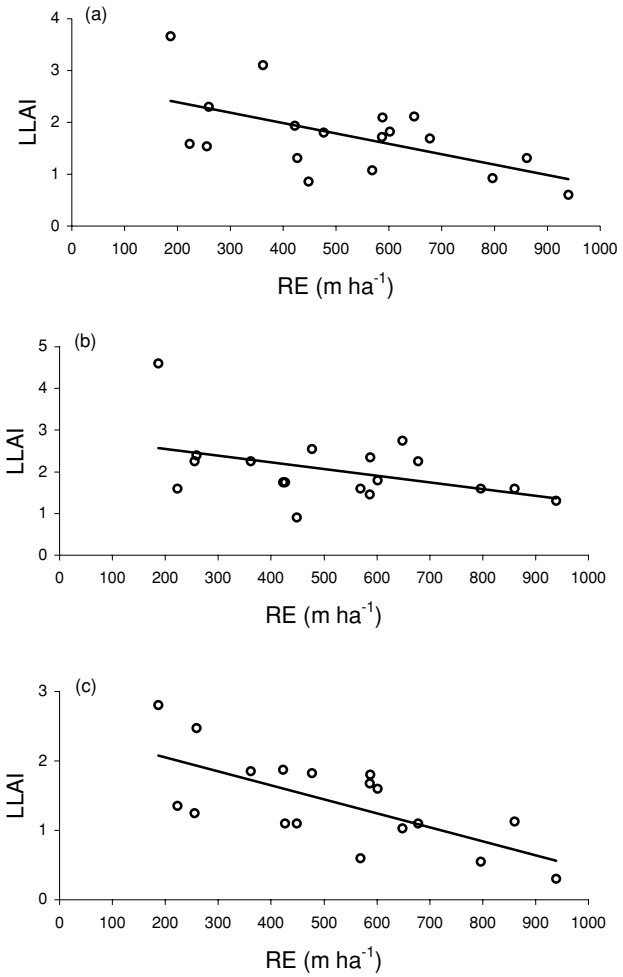


Figure 1. The relationship between Leaf Litter Area Index (LLAI) and Relative Edge length (RE) for (a) whole islands ($LLAI = -0.0018RE + 2.6$, $R^2 = 0.33$, $P < 0.05$), (b) just the leeward sides of islands ($LLAI = -0.0016RE + 2.8$, $R^2 = 0.17$, $P > 0.05$) and (c) for just the windward sides of islands ($y = -0.002x + 2.4$, $R^2 = 0.47$, $P < 0.005$).

These results are contrary to those found in studies of litter depth at BDFFP, where they found that greater wind exposure actually led to deeper litter accumulation (Sizer *et al.* 2000). There are several possible reasons for this

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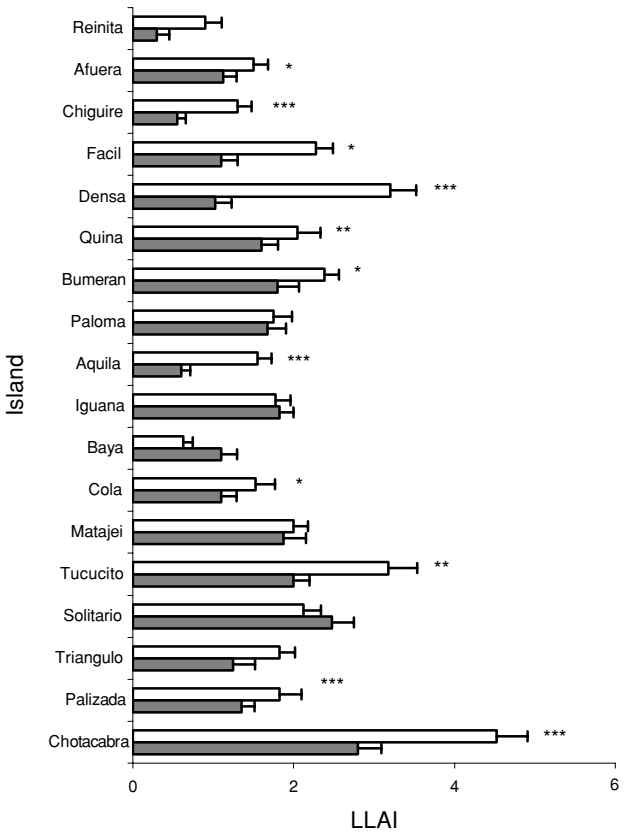


Figure 2. The mean Leaf Litter Area Index (LLAI) of leeward (clear) and windward (filled) sides of islands. Islands are shown in descending order of Relative Edge Length (RE). Error bars represent one SE. LLAI was significantly greater on the leeward than windward side on 11 of 18 islands (two-tailed t-test; * $P < 0.10$, ** $P < 0.05$, *** $P < 0.001$).

discrepancy. The habitat of BDFFP is an evergreen moist forest (Laurance *et al.* 1998), and thus the trees may be highly susceptible to desiccating winds. Drier conditions along the forest edges will cause drought-stressed trees to shed their leaves (Laurance *et al.* 2002, Sizer *et al.* 2000). In contrast, the habitat at Lake Guri is a semi-deciduous dry forest (Huber 1986, Terborgh *et al.* 1997). Trees that are adapted to these dry conditions should be less susceptible to drought stress, and thus wind exposure is not expected to lead to increased abscission of leaves. It is also possible that the deep litter along the edges of fragments at BDFFP is due to an accumulation of litter blown into the forest from the surrounding matrix habitat (a mixture of pasture and secondary growth). Finally the size of fragments used in this study is almost an order of magnitude smaller than the fragments studied at BDFFP (Sizer *et al.* 2000). I suspect that the larger fragments act as better wind barriers and thus less leaf material is blown away.

With continued deforestation and land conversion, an increasing percentage of the world's remaining forested habitat will inevitably become subdivided into isolated fragments and patches. Studies investigating the effects of habitat fragmentation have typically focused on changes in the population or community dynamics of the flora and fauna (Laurance & Bierregaard 1997). Comparatively few studies have examined the role of fragmentation in altering nutrient cycling. In this study of land-bridge islands in Lake Guri Venezuela, I have shown that fragmentation can cause significant changes in the quantity of accumulated litter. Given that leaf litter is one of the primary pathways for the cycling of nutrients from vegetation to soil, these changes are expected to strongly influence the rate at which nutrients are mineralized and made available to plants.

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