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NOTE: At the time of publication, author Fred Scatena was affiliated with the USDA Forest Service. Currently (June 2006), he is a faculty member in the Department of Earth and Environmental Science at the University of Pennsylvania.

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# Non-Indigenous Bamboo along Headwater Streams of the Luquillo Mountains, Puerto Rico: Leaf Fall, Aquatic Leaf Decay and Patterns of Invasion

## Abstract

The introduction of bamboo to montane rain forests of the Luquillo Mountains, Puerto Rico in the 1930s and 1940s has led to present-day bamboo monocultures in numerous riparian areas. When a non-native species invades a riparian ecosystem, in-stream detritivores can be affected. Bamboo dynamics expected to influence stream communities in the Luquillo Experimental Forest (LEF) were examined. Based on current distributions, bamboo has spread downstream at a rate of 8 m y<sup>-1</sup>. Mean growth rate of bamboo culms was 15.3 cm d<sup>-1</sup>. Leaf fall from bamboo stands exceeded that of native mixed-species forest by c. 30 (k = -0.021), and leaves from another abundant riparian exotic, *Syzygium jambos* (Myrtaceae) (k = -0.018), decayed at relatively slow rates when submerged in streams in fine-mesh bags which excluded macro-invertebrate leaf processors. In a second study, with leaf processors present, bamboo decay rates remained unchanged (k = -0.021), while decay rates of *S. jambos* increased (k = -0.037). Elemental losses from bamboo leaves in streams were rapid, further suggesting a change in riparian zone/stream dynamics following bamboo invasion. As non-indigenous bamboos spread along Puerto Rico streams, they are likely to alter aquatic communities dependent on leaf input.

## Comments

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## Non-indigenous bamboo along headwater streams of the Luquillo Mountains, Puerto Rico: leaf fall, aquatic leaf decay and patterns of invasion

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**ABSTRACT.** The introduction of bamboo to montane rain forests of the Luquillo Mountains, Puerto Rico in the 1930s and 1940s has led to present-day bamboo monocultures in numerous riparian areas. When a non-native species invades a riparian ecosystem, in-stream detritivores can be affected. Bamboo dynamics expected to influence stream communities in the Luquillo Experimental Forest (LEF) were examined. Based on current distributions, bamboo has spread downstream at a rate of 8 m y<sup>-1</sup>. Mean growth rate of bamboo culms was 15.3 cm d<sup>-1</sup>. Leaf fall from bamboo stands exceeded that of native mixed-species forest by c. 30% over a 10-mo study. Bamboo leaves ( $k = -0.021$ ), and leaves from another abundant riparian exotic, *Syzygium jambos* (Myrtaceae) ( $k = -0.018$ ), decayed at relatively slow rates when submerged in streams in fine-mesh bags which excluded macro-invertebrate leaf processors. In a second study, with leaf processors present, bamboo decay rates remained unchanged ( $k = -0.021$ ), while decay rates of *S. jambos* increased ( $k = -0.037$ ). Elemental losses from bamboo leaves in streams were rapid, further suggesting a change in riparian zone / stream dynamics following bamboo invasion. As non-indigenous bamboos spread along Puerto Rico streams, they are likely to alter aquatic communities dependent on leaf input.

**KEY WORDS:** bamboo, *Bambusa* spp., biological invasion, leaf decay, leaf fall, non-indigenous, Puerto Rico, riparian, *Syzygium jambos*, tropical headwater streams

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## INTRODUCTION

Non-indigenous species are homogenizing the world's biota at a rapidly increasing rate (Vitousek *et al.* 1996). Biological introductions can develop into monocultures, alter nutrient regimes, and even drive native species to extinction (Ruesink *et al.* 1995). Biological invasions have been documented as disrupting communities only where and when effects were severe and readily observable, or were directly influencing species loss (Mooney & Drake 1986, Pimm *et al.* 1995, but see Vitousek 1990). However, the majority of introductions may be neither direct in influence, nor temporally obvious, and can lead to loss of ecosystem function through indirect effects (Lodge *et al.* 1998). When an invasion involves a group unrepresented in the native system, communities and ecosystems may be readily altered (Vitousek 1986). In this paper, we consider the impacts of introduced bamboos in headwater rain forest riparian areas of Puerto Rico.

Partly as a result of physical heterogeneities in lotic systems, stream riparian communities possess structural and species compositional diversity (Covich 1988, Gregory *et al.* 1991). Nevertheless, riparian zones are also common corridors for spread of exotic plants (Naiman & Décamps 1997). Riparian plants restrict sunlight and primary production within the channel, but along forested headwater streams riparian leaf inputs provide energy sources for stream food webs (Vannote *et al.* 1980). Leaves deposited in streams can also be critical determinants of community structure by creating heterogeneous microhabitats for invertebrates (Cummins *et al.* 1989, Friberg & Winterbourn 1997). This terrestrial-aquatic linkage may be more pronounced in the tropics, where total leaf fall tends to exceed that of temperate forests (Benson & Pearson 1993).

In both tropical and temperate headwater streams, mixed species leaf fall is important in providing diverse sources of energy and benthic habitat structure (Dudgeon 1994, Irons *et al.* 1988, Wallace *et al.* 1997). In contrast, bamboos often form mono-specific stands in riparian zones (Chou 1981, Gadgil & Prasad 1984). Once established, bamboo can effectively exclude other plant species (Taylor *et al.* 1996). Similar to such replacement of diverse native forest by bamboo monocultures, disturbances which change the rate or quality of inputs to a stream often affect shifts in detritivores at several trophic levels in the aquatic web (Dudgeon 1994, Molles 1982, O'Connor 1998, Wallace *et al.* 1997).

Although the worldwide distribution of bamboo has been greatly modified by human intervention, little is understood about bamboo ecology (McClure 1993). The introduction of bamboo to the Caribbean National Forest (contiguous with the Luquillo Experimental Forest) in northeastern Puerto Rico in the 1930s and 1940s (White & Childers 1945), has led to expanding bamboo monocultures in several riparian areas. Since introduction, the bamboos have spread by vegetative reproduction through extensive rhizome networks, downslope transport and re-rooting of broken culms, and in 1996, by

flowering and seed-set for the first time on record (P. O'Connor and F. Wadsworth, *pers. obs.*). We provide the first study of bamboo ecology in Puerto Rico, and describe selected bamboo dynamics expected to affect aquatic consumers in Luquillo's tropical montane watersheds. Leaf fall rate, growth of rhizomally reproduced bamboo culms, spread of bamboo in a headwater riparian zone, and aquatic leaf decay including elemental loss are examined. We compare bamboo leaf decay and elemental loss rates in headwater streams to those of another common LEF riparian exotic, *Syzygium jambos* Alston (Myrtaceae). In a smaller scale decomposition study we also compare bamboo and *S. jambos* leaf decay rate to that of an LEF native, *Guarea guidonia* Sleumer (Meliaceae).

#### STUDY SPECIES

Most bamboo species (Gramineae) introduced to the Luquillo Experimental Forest (LEF) are in the tropical Asian genus *Bambusa* (*Bambusa vulgaris* Schrader ex Wendland, *B. longispiculata* Gamble ex Brandis, *B. tulda* Roxb. and *B. tuldoidea* Munro) (White & Childers 1945). Individuals of another tropical Asian species, *Dendrocalamus strictus* Nees, were also planted (L. Clark and F. Wadsworth, *pers. comm.*). Although bamboo was planted along roads to stabilize downhill slopes (White & Childers 1945), during major disturbances like hurricanes, extensive bamboo root systems can result in catastrophic slope failures when undercut (P. O'Connor, *pers. obs.*). Coinciding with low stream water levels, *B. vulgaris* and *D. strictus* can drop their leaves during drought. In their native ranges in Asia, these bamboos usually form secondary forests following shifting agriculture or other disturbances. Climate and soils are often considered primary factors in limiting bamboo productivity (Farrelly 1984, Numata 1979). Constant warm temperatures, high humidity, and evenly distributed rainfall in the LEF means that bamboo may have few natural barriers to expansion besides soil suitability. In coastal rain forests of Brazil, introduced *Bambusa* spp. and *Dendrocalamus* spp. dominate large regions with similar climate to the LEF (Numata 1979).

Leaf anatomy and growth patterns are similar among the five bamboo species introduced throughout the LEF (Soderstrom & Calderón 1979). All form clumps of culms on the landscape, with stalks reaching mature heights of 10–20 m. These similarities, in conjunction with their highly mixed distributions and the difficulty of identifying bamboo species without flowers or well-documented planting locations justify our combined treatment of the five bamboo species in this study as 'bamboo'. For comparison with aquatic leaf decay parameters of bamboo, we also examined leaves of *Syzygium jambos* (rose apple, jamrose), another exotic species forming riparian monocultures in the LEF. On Réunion Island in the Indian Ocean, *S. jambos* has invaded all streams on the humid coast, and excludes native plants, probably through allelopathy (C. Lavergne, *pers. comm.*). In several areas of the Luquillo mountains, the current riparian distribution of *S. jambos* can equal that of bamboo. In our second

and smaller scale decay study we included leaves of *Guarea guidonia* as a native species comparison. *G. guidonia*, a dicot, is common along the study reach on Olga stream at *c.* 200 m elevation.

#### METHODS

We focused on bamboo populations in and adjacent to the Bisley watersheds area of the National Science Foundation's Luquillo Experimental Forest (LEF) Long Term Ecological Research (LTER) site (18°30' N, 65°82' W). The Bisley watersheds are within a windward, subtropical wet-forest life zone dominated by secondary tabonuco (*Dacryodes excelsa* Vahl) type forest (Ewel & Whitmore 1973), and receive a mean annual rainfall of 3500 mm (Scatena & Larsen 1991). Terrain is steep, and characterized by high gradient stream channels and narrow drainage divides (Scatena & Lugo 1995). Headwater streams in Bisley have a highly variable hydrology in response to frequent rainfall events. Stream pools dominate habitats for aquatic macro-invertebrates. The native riparian forest has a diverse community structure, including herbaceous layers, ferns, and several layers of tree canopy which overhang stream channels. Bamboo will also overhang channels, however bamboo monocultures are noticeably simple in comparison to native LEF riparian forest because they lack an understory, and have a dense ground layer of leaf litter.

#### *Vegetative reproduction and culm growth in bamboo*

Ten culms from vegetatively reproducing bamboo clumps along the Bisley road were randomly selected and measured daily during July–August 1996. Standard diameter (DBH) tapes and telescoping poles were used to determine daily growth rates. Daily through fall (mm) was collected in two nearby ground gauges and compared with growth rates.

#### *Bamboo range expansion*

We surveyed 750 m of Bisley 3, a representative second-order headwater stream draining 35 ha in the Bisley watersheds. Locations of bamboo clumps within 5 m of the channel were mapped in reference to the planted source population on the Bisley road. An annual rate of downstream range expansion for bamboo was extrapolated. Total number of culms and mean culm DBH in each clump were used to estimate relative times since clump establishment.

#### *Leaf fall*

To compare rates at which leaves enter streams, a total of 24 plastic baskets with 0.25 m<sup>2</sup> openings were lined with fibreglass screening and randomly set at ground level in three plots under bamboo monocultures, and in three plots under adjacent native tabonuco-type forest within the Bisley watersheds. Litterfall was collected biweekly, from 20 August 1996 to 13 May 1997. Collected

materials were oven-dried at 65 °C to constant weight and sorted. Dry weights of fallen leaves are reported as  $\text{g m}^{-2} \text{d}^{-1}$ .

#### *Bamboo leaf chemical analyses*

Elemental concentrations in the bamboo leaf fall were determined. Chemical analyses were performed at the USDA Forest Service International Institute of Tropical Forestry laboratory in Río Piedras, Puerto Rico, following methods described in Scatena *et al.* (1996). Dried leaves were weighed to the nearest 0.1 g and ground with a Wiley mill through a 0.85-mm stainless steel wire sieve. After digestion with 30%  $\text{H}_2\text{O}_2$  and concentrated  $\text{HNO}_3$ , samples were analysed with a Beckman Spectra Span V plasma emission spectrometer for P, K, Ca, Mg, Al, Mn and Fe content. Nitrogen, C and S were analysed by dry combustion in a LECO CNS-2000. Carbon (as  $\text{CO}_2$ ), S (as  $\text{SO}_2$ ) and N (as  $\text{NO}_2$ ) were determined by infrared and thermal conductivity cells.

#### *Leaf decay in streams*

Two experiments to investigate the decay rates of bamboo and *S. jambos* leaves were carried out. The first, from June–August 1996, assessed leaf decay rates attributed to microbial and chemical processes. We used three accessible headwater streams in or adjacent to the Bisley watersheds (Bisley 3, Bisley 5 and Olga) with pools large enough to receive 70 treatment leaf packs. Because pools are typical leaf deposition sites, and important habitat for leaf processors, packs were submerged in a randomly selected pool in each stream. Four-gram leaf packs of freshly picked, oven-dried bamboo or *S. jambos* leaves were enclosed within 1-mm<sup>2</sup> mesh bags. The fine-mesh excluded macro-invertebrates and prevented particle loss due to stream flow. Five sets of seven bamboo packs, and five sets of seven *S. jambos* packs, were submerged with each set randomly assigned to a PVC pole secured in pool substrata. A total of 210 leaf packs (two species  $\times$  five replicates  $\times$  seven samples  $\times$  three streams), was placed in the streams. A first sample was collected 72 h after submergence, to quantify mass loss due to solute leaching. A randomly selected pack was removed from each pole (for a total of five bamboo leaf packs, and five *S. jambos* leaf packs) once a week from each of the three pools for 6 wk, beginning 1 wk after submergence. Packs were carefully rinsed in the laboratory to remove accumulated sediments and then leaves were oven-dried at 65 °C to constant weight, and weighed to the nearest 0.01 g. Daily decay rates were determined using decay constants (*k*) from negative exponential models (Petersen & Cummins 1974). Differences were analysed by ANOVA using SAS (1996). Leaves from this decay experiment, and oven-dried samples of freshly picked bamboo and *S. jambos* leaves were analysed for elemental concentrations following the same methods we used for elemental analyses of leaf fall.

The second decay study was conducted in January–February 1997. Only one

stream (Olga) was used during this second experiment because of the similarity in decay patterns observed across the three streams in the first study, and increased washout probability from unsettled weather patterns prior to this experiment. Leaves of bamboo, *S. jambos* and *Guarea guidonia* were decomposed without mesh bags to allow access to the leaves by macro-invertebrates. A total of 84 (three species  $\times$  four replicates  $\times$  seven samples) 4-g oven-dried leaf packs secured within tension clips was submerged in a headwater pool of Olga stream. As in the earlier experiment, packs rested on the bottom. Because no mesh bags were used, leaf fragments may have been broken off by stream flow as decay advanced. Samples were collected at the same intervals as in the first decay experiment, and similarly dried and weighed. Decay constants were analysed by analysis of variance (ANOVA) and differences among species were compared by least significance difference (LSD) using SAS (1996).

## RESULTS

### *Vegetative reproduction and culm growth in bamboo*

Culm growth rates increased over time during our sampling period. Diameter at breast height (DBH) of growing culms did not change over time. Vertical growth was rapid, with a mean growth rate of  $15.3 \text{ cm d}^{-1}$ . We found no apparent relationship between throughfall and growth (Figure 1). Daily growth minima for 50% of culms was during Hurricane Bertha on 9 July 1996.

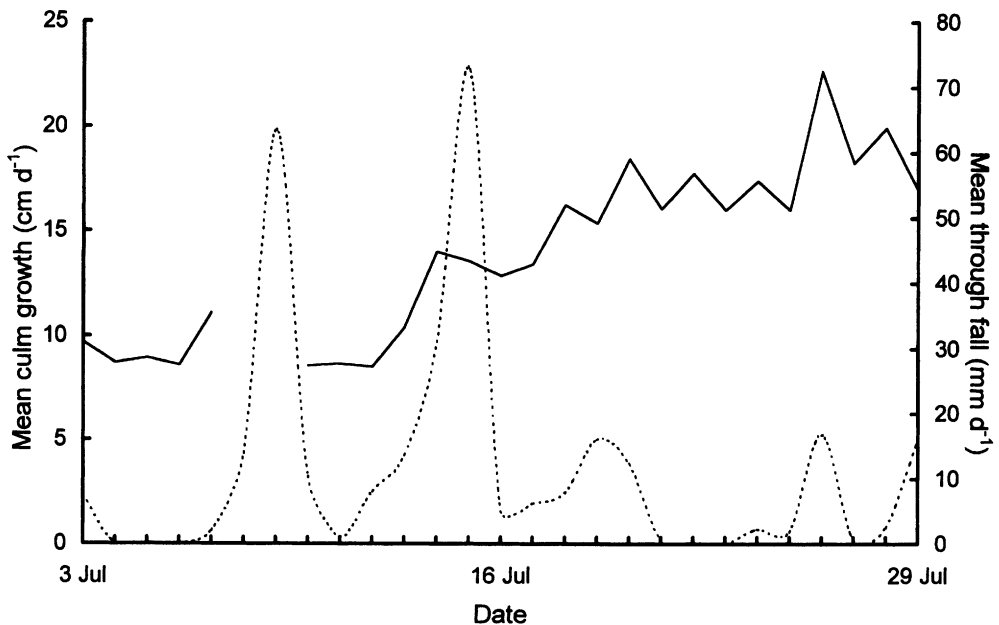


Figure 1. Comparison of mean culm growth rates of bamboo along the Bisley road (solid line), to daily throughfall rates (fine-dashed line) during July 1996, Luquillo Experimental Forest, Puerto Rico.



*Downstream spread of bamboo*

Bamboo clumps occurred along Bisley 3 until 430 m downstream from their original planting site on the Bisley road. Using 1945 as the average planting year, the bamboos have spread at an approximate rate of  $8 \text{ m y}^{-1}$ . Logistic regression revealed a relationship between mean culm DBH and number of culms per clump ( $r = 0.856$ ). No linear relationship was found between downstream distance from the Bisley road and size of bamboo clumps (Figure 2). The shortest distance between consecutive clumps occurred in a low-gradient reach, 170–194 m downstream of the road.

*Leaf fall*

From August 1996 to May 1997, mean leaf fall was  $1.62 \text{ g m}^{-2} \text{ d}^{-1}$ , for branches and  $1.10 \text{ g m}^{-2} \text{ d}^{-1}$  for mixed-species native forest. For the first 2 mo of this period leaf fall rates of bamboo exceeded those of mixed species forest in every sample collected (Figure 3). Concentrations of nutrients considered important to stream communities ( $\text{mg g}^{-1}$ ) were lower in bamboo than in native forest leaf fall (Figure 4).

*Leaf decay in streams*

Bamboo and *S. jambos* leaves enclosed in mesh bags decayed at similar rates (Figure 5). Negative exponential models and negative linear models to the

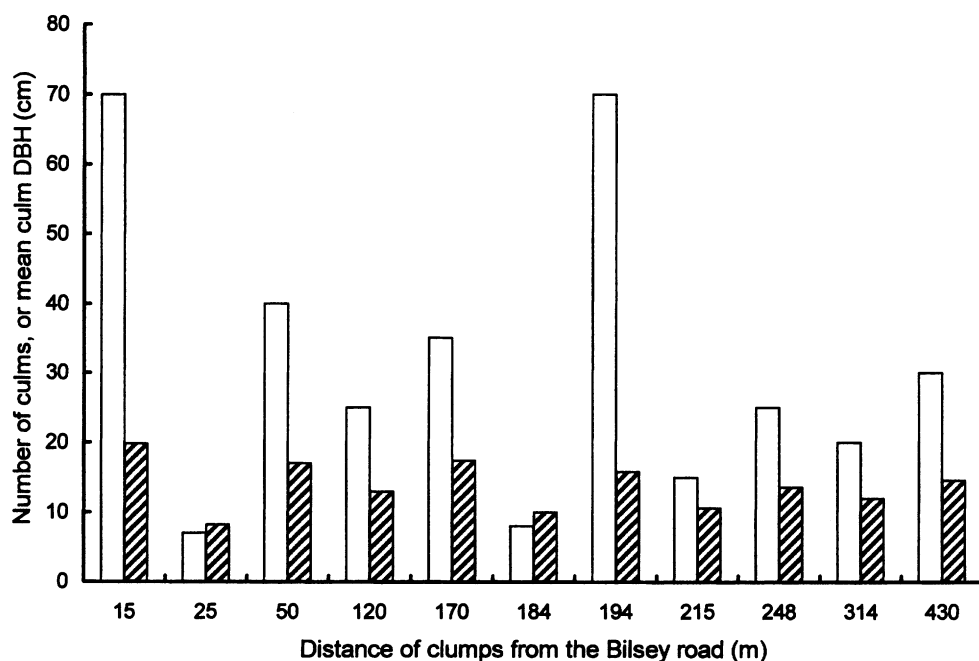


Figure 2. Changes in clump size with downstream distance, based on two measures (culms per clump, open bars; mean culm DBH, hatched bars), within a 5-m buffer zone of the Bisley 3 stream channel, Luquillo Experimental Forest, Puerto Rico.

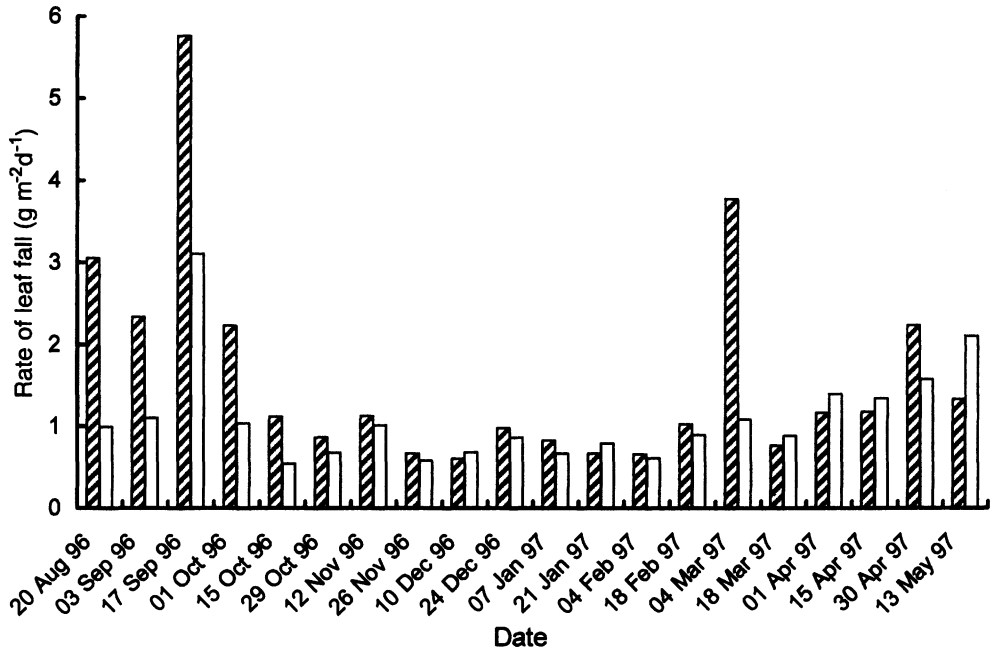


Figure 3. Mean daily leaf fall rates under bamboo (hatched bars) and mixed native forest stands (open bars) in the Bisley watersheds from August 1996 to May 1997, Luquillo Experimental Forest, Puerto Rico.

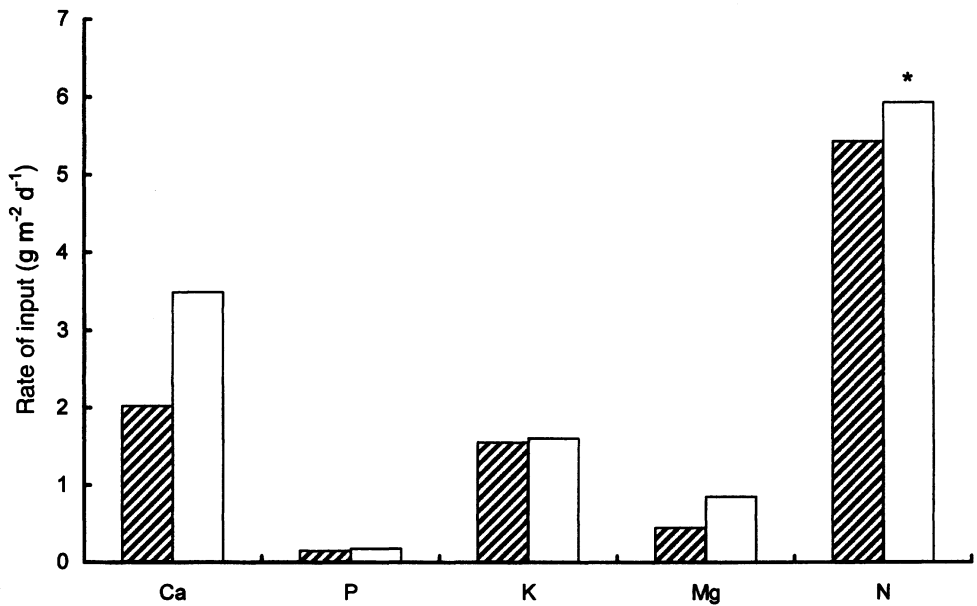


Figure 4. Input rates of selected elements in leaf fall within bamboo (hatched bars), and native mixed (open bars) forest stands in the Bisley watersheds, Luquillo Experimental Forest, Puerto Rico. \*, native forest leaf fall N from non-hurricane leaf fall from Lodge *et al.* (1991).

decay data provided similar fits of  $r^2 > 0.98$ . Decay constants ( $k$ ,  $\pm$  SE) from the exponential models were  $-0.021 \pm 0.002$  for bamboo, and  $-0.018 \pm 0.001$  for *S. jambos*. Decay constants did not differ between the two leaf types when decomposed in fine-mesh bags. Daily weight losses as described by linear models were  $-0.052 \pm 0.004$  g d<sup>-1</sup> for bamboo, and  $-0.051 \pm 0.002$  g d<sup>-1</sup> for *S. jambos*.

In the second decay study, decay constants ( $k$ ) for unbagged bamboo leaves (negative exponential model  $r^2 > 0.95$ ) were unchanged ( $-0.021 \pm 0.002$ ) from those in bags, but increased to  $-0.037 \pm 0.003$  for leaves of *S. jambos* (Figure 5). Decay rates were similarly approximated by linear models ( $r^2 > 0.95$  for bamboo;  $r^2 > 0.97$  for *S. jambos*), and weight losses using these models were  $-0.054 \pm 0.004$  g d<sup>-1</sup> for bamboo and  $-0.075 \pm 0.003$  g d<sup>-1</sup> for *S. jambos*. Leaves from the native tree species *Guarea guidonia* followed only a negative exponential model ( $r^2 > 0.99$ ), with  $k = -0.040 \pm 0.003$  (Figure 5). Rates among species differed significantly ( $F = 15.10$ ;  $df = 2, 9$ ;  $P < 0.010$ ). The LSD multiple comparison ( $\alpha = 0.05$ ,  $n = 4$ ) revealed that decay rates of bamboo leaves (mean  $k = 0.021$ ) were significantly slower than those of *S. jambos* (mean  $k = 0.037$ ) and *G. guidonia* (mean  $k = 0.040$ ). Decay rates for the latter two species were not significantly different.

#### *Nutrient dynamics of leaves in streams*

Elemental mobility from decaying bamboo leaves during the first 3 d were, in decreasing order of percentage loss, K, Ca, P, N and C. After 6 wk, elemental concentrations in bamboo leaves were, in decreasing order, C, N, P, Ca and K (Figure 6) (Table 1). In *S. jambos*, elemental mobility, beginning with greatest initial loss over the first 3 d were, in decreasing order, K, P, N, C and Ca. After 6 wk, highest elemental concentrations in *S. jambos* were, in decreasing order, Ca, N, C, P and K (Figure 6) (Table 1). Large increases in metal concentration occurred in leaves of both species (Table 1). Fresh bamboo leaves had higher Al, Fe and Mn concentrations than fresh *S. jambos* leaves.

## DISCUSSION

Rain forests of northeast Puerto Rico are held in stages of intermediate succession by disturbance events such as hurricanes, landslides and frequent stream spates (Covich *et al.* 1996, Lugo & Scatena 1996). As a result, the LEF contains naturally species-diverse systems, a characteristic strongly reflected in its riparian zones (Reagan & Waide 1996). If an exotic monoculture does not differ structurally from a native forest, it may not necessarily disrupt community functions (Lugo 1992). Bamboo and its leaves, however, clearly possess influential characteristics among forest communities and leaf inputs to streams in the LEF.

#### *Rhizome reproduction and culm growth in bamboo*

Growth of bamboo culms in the LEF was typical of bamboo in other regions in that culm DBH did not change with increasing height (Christianty *et al.*

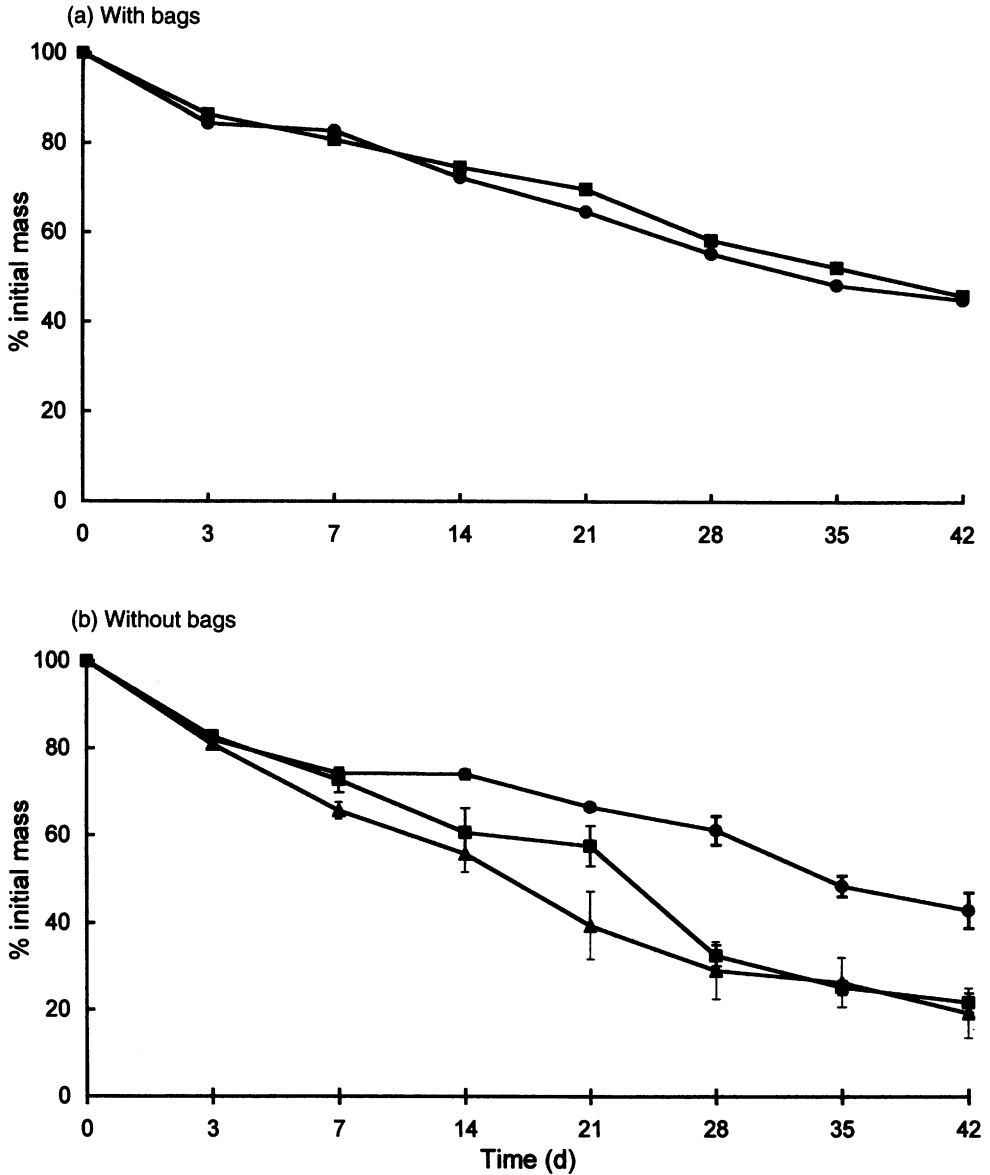


Figure 5. Decay (loss in mass) over 6 wk for leaf packs of (a) two exotic species, in fine mesh (1-mm<sup>2</sup>) bags, and (b) these plus a native forest species, all without bags, in three headwater streams in the Luquillo Experimental Forest, Puerto Rico. Symbols for species: Bamboo (●), *Syzygium jambos* (■) and *Guarea guidonia* (▲). In (a), the SEs of the means ( $n = 15$ ) were too small to be visible on the graph; they ranged from 0.01 to 0.04 for bamboo, and from 0.01 to 0.02 for *S. jambos*; in (b) the SEs are based on means with  $n = 4$ .

1996). At a mean growth rate of 15.3 cm d<sup>-1</sup> in height, the culms we measured attained mature heights of 10–20 m in *c.* 4 mo. Because rainfall in the LEF is distributed fairly evenly throughout the year (Scatena & Larsen 1991), culm production and growth may occur on a continual basis. Regression of daily

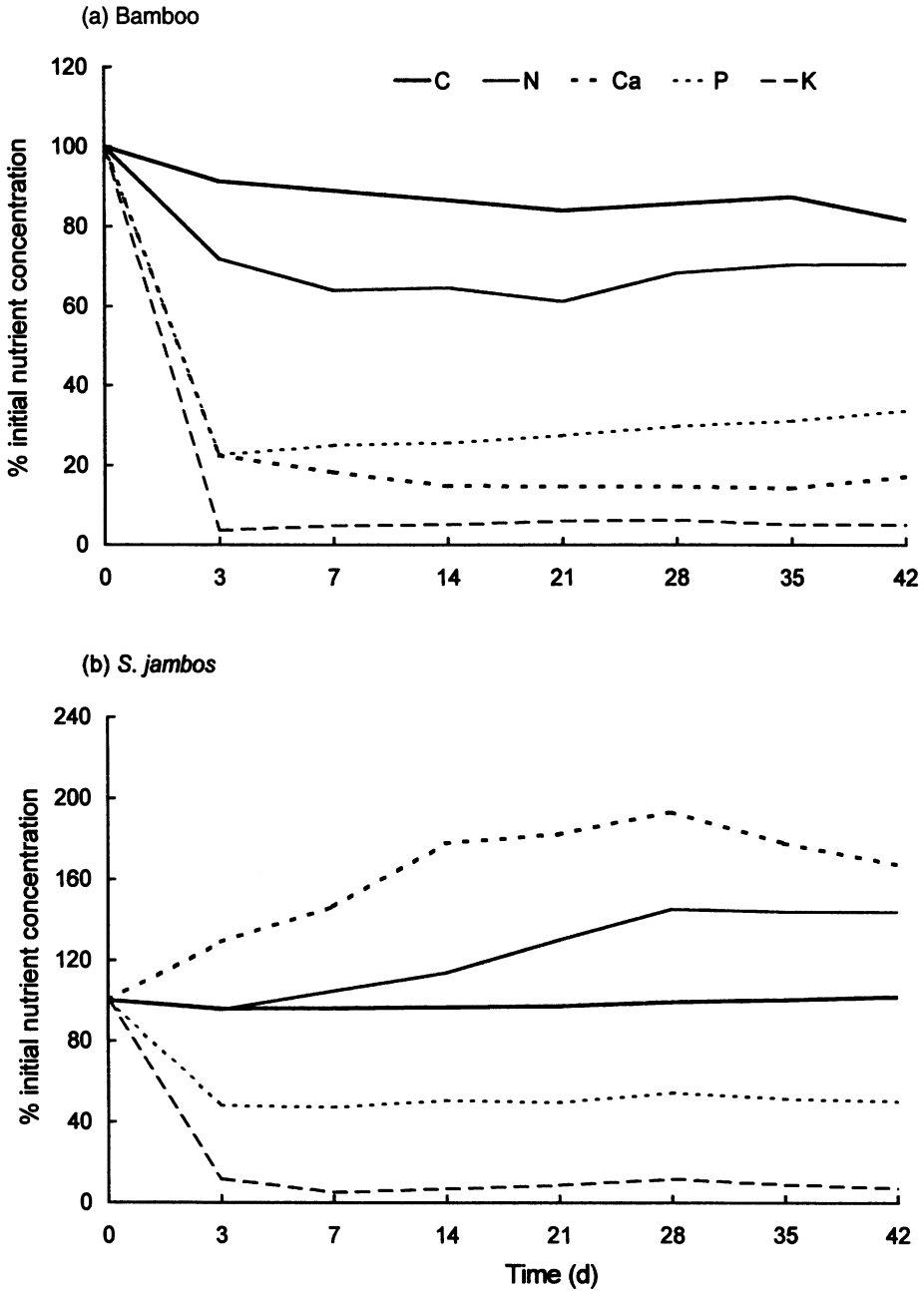


Figure 6. Changes in mean concentrations of selected elements (n = 15) in (a) bamboo leaves and (b) leaves of *Syzygium jambos*, over 6 wk of decay in three headwater streams from June–August 1996, Luquillo Experimental Forest, Puerto Rico.

Table 1. Initial concentrations ( $\text{mg g}^{-1}$ ) of selected elements in green leaves of exotic riparian trees, and mean percentages of initial concentration remaining in the leaves ( $\% \pm 1 \text{ SE}$ ) after 6 wk of aquatic decay in Luquillo Experimental Forest headwater streams, Puerto Rico.

Element	Initial concentration ( $\text{mg g}^{-1}$ )		% remaining after 6 wk	
	Bamboo <sup>1</sup>	<i>Syzygium jambos</i>	Bamboo <sup>1</sup>	<i>Syzygium jambos</i>
Ca	8.16	6.65	17.21 $\pm$ 2.57	167.39 $\pm$ 9.21
P	0.93	0.75	33.80 $\pm$ 8.99	50.35 $\pm$ 2.54
Mg	1.51	3.22	82.12 $\pm$ 34.97	47.63 $\pm$ 3.65
K	12.09	8.06	5.11 $\pm$ 0.73	7.10 $\pm$ 0.31
C	456.55	532.70	81.50 $\pm$ 4.75	101.81 $\pm$ 0.13
S	4.76	1.97	3.94 $\pm$ 0.36	93.31 $\pm$ 2.53
EN	24.20	14.40	70.52 $\pm$ 4.74	144.11 $\pm$ 2.23
Mn	1.01	0.02	18.14 $\pm$ 5.18	650.77 $\pm$ 23.68
Al	0.94	0.07	769.99 $\pm$ 122.97	1443.15 $\pm$ 359.05
Fe	0.55	0.05	1327.02 $\pm$ 313.02	4525.23 $\pm$ 448.26

<sup>1</sup>Bamboo is used to generally refer to leaves from five possible species of bamboos (*Bambusa vulgaris*, *B. tulda*, *B. longispiculata*, *B. tuldooides* and *Dendrocalamus strictus*).

growth rates on through fall showed no strong correlation with culm growth, however as is visible in Figure 1, growth rates were greater during decreased through fall following several heavy rain events early in the measured growth period. Half of the culms registered daily growth minima during Hurricane Bertha (9 July 1996), supporting an observation by Numata (1979), that winds can cause excessive transpiration contributing to a slowing of growth.

#### *Downstream spread of bamboo*

Distribution of bamboo along the Bisley 3 stream revealed that bamboo spread in LEF riparian zones is a stochastic process which does not lend itself easily to invasion modelling efforts (see Hastings 1996). A greater count and mean DBH of culms within a bamboo clump is expected to reflect a longer time since clump establishment. If bamboos were proceeding downstream in a predictable manner, we would expect to find the smallest clumps furthest from the source population. However, there was no correlation between clump size and distance from the source population. Bamboo clumps were found as far as 430 m downstream from the Bisley road, and the largest clumps were at 15 m and 194 m downstream. Bamboo spread is likely to be a function of complex disturbance events such as high flows and hurricanes. High stream flows and winds may dislodge or break upstream culms, which can re-root downstream. A lack of planting records precludes an exact model of spread, but we offer 8  $\text{m y}^{-1}$  as an estimated maximum annual rate of downstream range expansion.

#### *Leaf fall*

Leaf fall patterns determine rates at which energy or habitat structure may be available for benthic stream fauna. Leaf fall rates ( $\text{g m}^{-2} \text{d}^{-1}$ ) in bamboo plots exceeded those in nearby native forest plots by *c.* 30%. Extrapolating our results to a period of an entire year suggests that annual bamboo leaf fall in the LEF would total 5877  $\text{kg ha}^{-1}$ . This total is within a range of recently

Table 2. Recently reported bamboo leaf fall rates.

Species	Location	Status	Leaf fall (kg ha <sup>-1</sup> y <sup>-1</sup> )	Source
<i>D. strictus</i>	India	native	4360	Tripathi & Singh (1995)
	India	native	5900	Tripathi & Singh (1996)
<i>Phyllostachys nigra</i>	Japan	native	5840	Isagi <i>et al.</i> (1993)
<i>P. pubescens</i>	Japan	introduced	4410	Isagi <i>et al.</i> (1995)

reported rates for bamboos in other areas (Table 2). Typically, native LEF forest leaf fall rates are lowest during October and November (Zou *et al.* 1995). We found that bamboo leaf fall rates were greater than those of native forest stands for all samples collected from August to November 1996, suggesting an atypical influx of leaves to streams with riparian bamboo during a period when fewer leaves typically fell. Extreme leaf fall values measured for the 2 wk prior to 17 September 1996 are most likely affected by the nearby passage of Hurricane Hortense.

#### *Leaf decay in streams*

A loss in diversity of leaf breakdown rates is associated with a loss in diversity of leaf species, and can result in changes to stream metabolism (Petersen & Cummins 1974). Mass loss from leaves of bamboo and *S. jambos* followed general aquatic leaf decay patterns in that an initial period of rapid leaching was followed by more constant mass loss over time (Webster & Benfield 1986). Linear models of decay suggest constant loss of weight over time and fit decay patterns best when macroinvertebrate processing or mechanical breakdown are minimal. Linear models, as well as the more traditional negative exponential models of aquatic decay adequately explained mass loss from leaves in our fine-mesh bag experiment. Decay rates dependent upon chemical and microbial processes alone did not differ between bamboo and *S. jambos*, although leaf chemistry and elemental release patterns did differ between the two leaf types. Bamboo leaves rapidly leached elements compared to *S. jambos*. The discrepancy may suggest that a greater proportion of the insoluble leaf structure in bamboo is unprocessed by microbes. Because a large amount of C is fixed per unit N or P assimilated by bamboo, their leaves are believed to be structurally complex (Soderstrom & Calderón 1979, Tripathi & Singh 1994).

In the presence of macro-invertebrates, leaf quality can influence mass loss (Basaguren & Pozo 1994). Without mesh bags, decay rates of bamboo leaves were not greater than rates measured in fine-mesh bags, suggesting a minimal influence of macro-invertebrates on bamboo decay. Stream consumers may not make direct use of bamboo leaves for food. Complex internal structures in bamboo leaves may also reduce losses of leaf mass due to mechanical processing. In contrast, decay rates of *S. jambos* did increase, suggesting impacts of macro-invertebrates or leaf particle loss from mechanical processing.

We used freshly picked leaves for the decay studies, whereas naturally senesced leaves could have a significant portion of their nutrients translocated

to culms prior to release (54–69% of N, P and K in *D. strictus*; Tripathi & Singh 1994). Regardless of nutritional quality, unless leaves are washed out by high flows, slower decay rates for bamboo suggest that bamboo leaves may provide submerged habitat structure longer than leaves of *S. jambos* or native tree species (Padgett 1976).

#### *Nutrient dynamics of leaves in streams*

By directly affecting nutrient availability and toxicity of certain ions to biota (Laskowski *et al.* 1995), elemental concentrations in leaves can impact the use of leaves as food and habitat. Palatability of leaves to stream consumers is dependent on a combination of conditions, including the initial nutrient status of the leaves themselves, and their level of conditioning by aquatic microbes. During terrestrial decay of bamboo in dry savannas of India, there are marked accumulations of N and P (Tripathi & Singh 1995). During aquatic decay in the LEF, we found these nutrients to be rapidly leached from bamboo leaves. Normally, aquatic microbes attached to decomposing leaves will fix N from the stream water. Leaves from non-indigenous eucalyptus monocultures altered stream dynamics in headwater drainages in Portugal (Abelho & Graça 1996). Nevertheless, during aquatic decay the eucalyptus leaves immediately accumulated N, suggesting some amount of microbial conditioning and N mutabilis. We found bamboo leaves in LEF streams rapidly lose N, suggesting little or no biotic processing. Poor nutrient enrichment of leaves in streams of the LEF is unlikely to be a consequence of low elemental concentrations in the stream water, because *S. jambos* leaves in the same pools as bamboo readily accumulated N and other elements. In another Puerto Rico stream, Justiniano & Betancourt (1989) report that seven aquatic fungi species were dominant in processing of *S. jambos* leaves. Unpublished data suggest different fungi species colonize bamboo (C. Betancourt, *pers. comm.*). Elemental increases in *S. jambos* may have resulted from stronger abilities of colonizing fungi and bacteria for active elemental uptake.

There is a net loss of N from the Luquillo Forest, largely attributable to dissolved organic nitrogen (DON) in streams (McDowell & Asbury 1994). Leaf litter is an important regulator of  $\text{NO}_3^-$  through the immobilization of dissolved N in forest run-off. If bamboo leaves and their associated aquatic microbes cannot immobilize N,  $\text{NO}_3^-$  losses may increase as bamboo spreads. Although there is a possibility that we missed N immobilization in bamboo leaves, this omission is unlikely. Concentrations of N in leaves of *S. jambos* increased after only 3 d. After 6 wk the increase exceeded 50%. Bamboo leaves had a limited immobilization of N by day 28, but after 42 d N concentrations were still below 75% of initial concentration. There is also a net loss of P from the LEF (McDowell & Asbury 1994). Concentrations of P in green bamboo leaves ( $0.90 \text{ mg g}^{-1}$ ) exceed those in green leaves of native LEF dicots ( $0.64 \text{ mg g}^{-1}$ ). However, in fallen bamboo leaves, P concentration is lower than in native forest leaf fall. Significant amounts of nutrients (N, P and K) can be retained by



bamboo culms prior to leaf fall (Totey *et al.* 1993). Bamboo may conserve P in this forest system by decreasing rates of P transfer in leaf fall to streams.

Potassium and calcium are important elements for stream macro-invertebrates, for example, in the rapid construction of chitinous exoskeletons following a molt. A rapid loss of K from both bamboo and *S. jambos* leaves during aquatic decay was expected because nutrients such as K which are not associated with leaf structure often are leached rapidly (Laskowski *et al.* 1995, Tripathi & Singh 1992). However, because Ca is commonly bound in leaf structures of most plants, leaching losses would not have been expected. Bamboo leaves lost more than 75% of initial Ca concentration in the first 3 d of decay. Leaves of *S. jambos* however retained Ca, with additional amounts accumulated almost immediately. Also important in influencing use or non-use of leaves by aquatic invertebrates, was a rapid increase in metals concentrations (Al and Fe) in bamboo leaves. Although leaves were consistently and carefully cleaned prior to analyses, potential binding of micro-fine stream sediments to decaying leaves is a natural part of the aquatic decay process and may partly explain increases in metal concentrations (F. Scatena, *pers. comm.*).

Introduced bamboos in riparian areas of the Luquillo Mountains may affect native stream macro-invertebrates through alteration of food resources and habitat typically provided by leaf inputs from native, mixed-species riparian forests. We found non-indigenous bamboo leaf fall exceeds that of native mixed forests, and where bamboo occurs in riparian zones, bamboo leaves undergo rapid leaching of elements during aquatic decay. We found no difference between decay rates for bamboo in the presence and absence of aquatic macro-invertebrate consumers, suggesting bamboo may not be utilized as an allocthonous food resource and negatively impacts food availability in stream pools dominated by riparian bamboo. Relatively slow rates for bamboo leaf decay suggest a considerable residency time for these leaves in stream pools, extending their potential influence on aquatic community structure. The continued downstream transport and re-rooting of broken segments of bamboo, rapid rhizome reproduction and growth, and most recently their successful flowering and seeding may accelerate bamboo expansion into currently native riparian areas. Frequent natural disturbances in the LEF are certain to influence these processes, and provide a recommended area of research into bamboo's potential impacts forest-wide. Direct comparisons of aquatic decay and nutrient loss of bamboo leaves to leaves of additional LEF riparian species are also needed. As non-indigenous bamboo expands its range in riparian areas of Puerto Rico, a decline in riparian species diversity may result in alteration of headwater stream communities dependant on a close linkage between riparian forests, and in-stream food and habitat resources.

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