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Effects of litter diversity on decomposition and biological colonization of submerged litter in temperate and tropical streams

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Abstract. Detrital food webs of woodland streams depend on terrestrial litter input and, thus, are susceptible to changes in riparian cover. We assessed effects of litter species richness and quality on decomposition and associated biological communities in temperate deciduous forest and tropical rainforest streams. Three native litter species were incubated in each stream in all combinations (7 litter treatments, 3 richness levels) in coarse- (invertebrate access) and fine-mesh bags (no invertebrate access) and were sampled 5 times over 74 (temperate stream) or 94 d (tropical stream). Decomposition, and fungal biomass, sporulation, and species richness were measured for each treatment. *Alnus glutinosa* litter was incubated in both streams to assess effects of environmental and biological differences between streams on litter decomposition. Biological colonization (number of fungal species, fungal biomass) and activity (conidial production) were lower in the tropical than the temperate stream, despite its higher water temperature (24 vs 8°C). Mass loss for individual species reached 95% in the temperate and 60% in the rainforest stream. Decomposition rates in mixtures were unaffected by litter richness but could be predicted from their initial N, phenol, and lignin concentrations (leaf quality). In the temperate stream, *Alnus* decomposition in coarse-mesh bags was positively related to litter richness, and *Alnus* stimulated decomposition of mixtures. Microbial O_2 consumption, fungal biomass accrual, aquatic hyphomycete sporulation rate and richness, and shredder abundance and richness were insensitive to litter richness. In the temperate stream, presence of tough litter inhibited invertebrate colonization of mixtures, whereas in the tropical stream, presence of soft litter stimulated invertebrate colonization of mixtures. Litter quality (species identity), not richness, was the main controller of decomposition of litter mixtures, and decomposition of litter in mixtures may differ from decomposition of individual species. Thus, disappearance or introduction of key species might affect organic matter processing in streams.

Key words: biodiversity-ecosystem function relationship, litter richness, litter decomposition, temperate stream, tropical rainforest stream.

The current rate of species loss is of great concern because the planet is undergoing a 6th wave of extinctions, which most consider anthropogenically driven, and because our knowledge about the relationship between species diversity and ecosystem function is still incipient (Chapin et al. 1998, Gessner et al. 2004, Cardinale et al. 2006). The relationship between the diversity of primary producers and primary production is positive (e.g., Cardinale et al. 2007), but the relationship between litter diversity and decomposition, the complementary ecosystem process to primary production in the C cycle, is still unpredictable (Catovsky et al. 2002).

In small woodland streams, where primary production is reduced by heavy shading from riparian vegetation, food webs acquire most of their energy and C from terrestrially derived litter (Vannote et al. 1980). Transfer of this C to higher trophic levels is promoted by decomposers, which mineralize organic C, incorporate it into biomass that is available to higher-level consumers, and promote transformation of litter into fine particulate organic matter to be used downstream by filter-feeders and gatherers (Quinn et al. 2000, Hieber and Gessner 2002, González and Graça 2003, Pascoal and Cássio 2004, Jonsson and Malmqvist 2005). Soft, high-quality (low C:N) substrates are

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preferentially colonized and degraded by aquatic hyphomycetes and invertebrate detritivores (Canhoto and Graça 1995, 1996, Ferreira et al. 2006b, Swan and Palmer 2006, Bastian et al. 2007). Because litters differ in quality and decomposers have preferences for high-quality substrates, changes in riparian vegetation composition and diversity can affect aquatic communities (Wood-Eggenschwiler and Bärlocher 1983, Read and Barmuta 1999, Rajashekhar and Kaveriappa 2003, Laitung and Chauvet 2005), and thus, litter-processing rates and ecosystem functioning (Kennedy and Hobbie 2004, Lecerf et al. 2005, 2007a, Riipinen et al. 2009).

Forest tree diversity throughout the world has been decreasing via substitution of forests with monocultures of tree species, degradation of riparian corridors by agricultural and industrial activities and urban settlements, and invasion by fast-growing, low-demand alien species (Royer et al. 1999, Graça et al. 2002, Aguiar et al. 2007, van Wilgen et al. 2007). This reduction in plant diversity might be of greatest concern in tropical areas, where the rate of species loss is thought to be the highest (Montagnini and Jordan 2005). Reduced plant diversity is likely to affect litter decomposition rates via changes in the decomposition environment, changes in litter species composition, and reduced consumer diversity (Hector et al. 2000, Hobbie et al. 2006, Miyamoto and Hiura 2007). Understanding the relationship between litter diversity and litter decomposition is important because changes in this basic ecosystem process will be reflected in the rate at which C and nutrients are cycled.

The effect of litter diversity on decomposition depends on litter quality and incubation conditions (Lecerf et al. 2011). The invertebrate density associated with litter can increase, decrease, or remain unaltered when litter diversity increases (Blair et al. 1990, Leroy and Marks 2006, Taylor et al. 2007, Abelho 2009, Kominoski and Pringle 2009, Sanpera-Calbet et al. 2009), and microbial activity seems to depend on litter quality and season (Kominoski et al. 2007, 2009, Taylor et al. 2007, Gonçalves and Canhoto 2009).

We evaluated the effect of litter richness (a surrogate for diversity) and litter quality on the decomposition and associated biota of 3 native litter species incubated individually and in all possible combinations in contrasting stream environments in a temperate deciduous forest stream (Portugal: low riparian tree richness) and in a tropical rainforest stream (Ecuador: high riparian tree richness). We used only 3 richness levels, which is a realistic simplification (e.g., Bastian et al. 2007), for logistic reasons. Our study is one of the first in which the effect of litter diversity on litter decomposition was assessed in a tropical stream (but see Moretti et al. 2007 for a Cerrado stream and Dudgeon and Gao 2011 for a Hong Kong stream). We also assessed the effect of litter richness on biological colonization and microbial activity associated with submerged decomposing litter. We used the same litter species (*Alnus glutinosa*) to compare litter decomposition, corrected for differences in water temperature, in temperate and tropical streams to shed light on the main mechanisms and environmental factors that affect this process in both systems. Last, we assessed the relationship between litter richness and litter decomposition by comparing decomposition of litter species incubated individually and in mixtures, as suggested by Ostrofsky (2007). Results from this design are less ambiguous than those from decomposition of entire litter mixtures, in which opposing effects of component species might mask an effect of litter diversity (Leff and McArthur 1989, Prescott et al. 2000, Gonçalves and Canhoto 2009, Sanpera-Calbet et al. 2009).

Decomposition of individual litter species was expected to benefit from litter mixing because of complementary effects arising from, e.g., nutrient transfer from nutrient-rich to nutrient-poor species that would enhance microbial colonization of nutrient-poor species when in mixture, attraction by nutrient-rich species of detritivores that also would feed on neighboring nutrient-poor species, or from attraction by recalcitrant litter of invertebrates seeking shelter in more stable substrates that would also feed on the neighbor labile litter. However, leaching of inhibitory compounds (e.g., phenols) from litter could deter colonization of neighbor litter species. Increased resource diversity was expected to lead to enhanced diversity of decomposers and detritivores. Decomposition of *Alnus* was expected to be faster at the warmer tropical stream than at the cooler temperate stream.

Methods

Study sites

The effect of litter richness on litter decomposition and associated biota was assessed in a temperate deciduous forest and a tropical rainforest stream. The temperate stream, Ribeira do Candal (Mondego River catchment), is on Lousã Mountain, central Portugal (lat 40°4′44″N, long 8°12′10″W; 620 m asl) where the 2006 mean minimum and maximum air temperatures were 11.1 and 21.3°C, respectively, and precipitation was 913 mm. This 2nd-order stream drains an area of 0.8 km^2 covered by mixed deciduous forest dominated by chestnut trees (*Castanea sativa* Mill.), where human activity is low. The bedrock is schistose and

TABLE 1. Mean (±1 SE, $n = 6$ dates except for water temperature) water and channel characteristics of the temperate deciduous forest (Portugal, 8 January–19 March 2007) and tropical rainforest (Ecuador, 17 March–19 June 2007) streams during the decomposition experiment. Water temperature was recorded hourly. na = not assessed.

Water variables	Temperate stream	Tropical stream	Method
Temperature (°C)	8.2 ± 0.4	24.1 ± 0.2	Hobo data loggers recording temperature hourly (HOBOware, Onset Computer Corp., Massachusetts)
Conductivity (μS/cm)	26.5 ± 1.7	70.3 ± 10.4	Handheld meter (WTW LF 330, WTW, Germany)
Alkalinity ($mgCaCO_3/L$)	4.9 ± 0.2	na	Titration with 0.02 N H_2SO_4 to an endpoint of pH 4.5 (APHA 1995)
O_2 (%)	113.8 ± 5.3	53.2 ± 9.6	Handheld meter (WTW OXI 92, WTW, Germany)
pH	6.5 ± 0.3	7.1 ± 0.2[a]	Field equipment (Portugal: JENWAY 3310, Bibby Sci. Ltd., UK; Ecuador: 4-Star Orion pH/conductivity portable meter, Carlsbad, California)
NH_4^+ (μg/L)	<10	27 ± 9	Ionic chromatography (Dionex DX-120, Sunnyvale, California)
NO_2^- (μg/L)	30 ± 21	na	Ionic chromatography (Dionex DX-120, Sunnyvale, California)
NO_3^- (μg/L)	445 ± 92	350 ± 80	Ionic chromatography (Dionex DX-120, Sunnyvale, California)
Width (m)	1.9 ± 0.12	4.7[b] ± 1.56	Measuring tape
Depth (m)	0.13 ± 0.00	1.14[c] ± 1.36	Measuring tape
Velocity (m/s)	0.19 ± 0.05	na[d]	Flow meter (Portugal: VALEPORT 15277, Valeport Ltd., UK; Ecuador: GW Water Logger model WL16 and Global Water flow probe model FP201, Gold River, California)
Discharge (m^3/s)	0.04 ± 0.02	na[d]	Computed as width × depth × velocity

[a] In a parallel study, we sampled pH for 3 consecutive days and recorded values between 4 and 7 (Capps et al. 2011)

[b] Width was similar at both stream sites at the beginning of the experiment but varied enormously at the tropical site because of normal seasonal variation in discharge

[c] Flow events in the stream are triggered by floods in the large Tiputini River, so water depth may range from several cm to >2 m in <1 d, and velocity may be ~0 when the water level in the Tiputini rises

[d] In the tropical stream, water velocity was very low (or sometimes 0) and impossible to measure accurately

the stream substrate is composed mainly of cobbles and pebbles. The stream generally flows year round, but may dry during extremely hot and dry summers. During the study period, the stream water was ~8°C, circumneutral, soft, well oxygenated, with low nutrient concentrations (Table 1). The tropical rainforest stream, Estero Numa (lat 00°38′393″S, long 076°08′905″W; 263 m asl), is part of the Tiputini River watershed in the northeastern Ecuadorian Amazonian region, at the site of the Tiputini Biodiversity Station of the Universidad San Francisco de Quito (TBS-USFQ). Annual precipitation varies between 2500 and 3200 mm, and daily temperature ranges between 24 and 27°C through the year (TBS-USFQ, unpublished data). Drier months are December to January (~80 mm/mo), and months with higher rainfall are May to June (~400 mm/mo; TBS-USFQ unpublished data). Estero Numa is a 1st-order stream that drains primarily lowland tierra firme tropical rainforest. This forest is part of the buffer zone of the Yasuni National Park, a Biosphere Reserve Site (Finer et al. 2009), and is currently subject to a very low degree of human intervention. Tree diversity in this tropical forest is extremely high (Pitman et al. 2002). Some of the most common riparian trees along the stream are *Inga* sp., *Triplaris* sp., *Zygia* sp., *Ficus* sp., and *Cecropia* sp. Estero Numa has strong hydrological variations in response to the heavy rains that are frequent in lowland Amazonia. Typical soils in this area are oxisols with low nutrient concentrations and high % silt and clay. Water chemistry varies with changes in hydrology. During the study, water was slow-flowing and poorly oxygenated (Table 1).

Litter decomposition

Three litter species native to each region were incubated, individually and in 2- and 3-species mixtures, in each stream to assess the effect of litter richness on litter processing and associated biota. In Portugal, leaves of alder (A; *Alnus glutinosa* (L.) Gaertn.), chestnut (C; *Castanea sativa* Mill.), and oak (Q; *Quercus robur* L.) were collected just after abscission in autumn 2006, air-dried at room temperature, and stored until needed. In Ecuador, leaves of guava (I; *Inga punctata* Willdenow), Fernán Sánchez (T; *Triplaris dugandii* Brandbyge), and Bushillca (Z;

TABLE 2. Mean (±1 SE) initial litter toughness (force needed to perforate a leaf sample) and chemical quality of the 6 litter species used in the decomposition experiment in the temperate deciduous forest (Portugal) and tropical rainforest (Ecuador) streams. Comparisons were made within each stream. Litter types with the same letter are not significantly different (Tukey's test, $p > 0.050$).

	Temperate stream			Tropical stream		
Litter variables	*Alnus glutinosa*	*Castanea sativa*	*Quercus robur*	*Inga punctata*	*Triplaris dugandii*	*Zygia cataractae*
Pressure (g/mm^2)	100.11 ± 2.78^{a}	128.46 ± 6.17^{b}	196.32 ± 8.82^{b}	241.10 ± 14.90^{B}	103.50 ± 0.97^{A}	307.66 ± 20.57^{C}
N (% AFDM)	1.45 ± 0.19^{a}	1.24 ± 0.11^{a}	1.21 ± 0.04^{a}	1.79 ± 0.32^{A}	1.69 ± 0.11^{A}	2.23 ± 0.11^{A}
P (% AFDM)	0.031 ± 0.004^{ab}	0.026 ± 0.008^{a}	0.053 ± 0.002^{b}	0.025 ± 0.001^{A}	0.034 ± 0.002^{B}	0.056 ± 0.002^{C}
Lignin (% AFDM)	37.15 ± 1.46^{a}	37.36 ± 0.22^{a}	35.38 ± 0.85^{a}	44.06 ± 0.14^{C}	30.79 ± 0.35^{A}	43.01 ± 0.21^{B}
Phenols (% AFDM)	7.90 ± 0.25^{a}	7.77 ± 0.74^{a}	15.70 ± 0.41^{b}	2.19 ± 0.06^{A}	6.82 ± 0.38^{B}	7.66 ± 0.16^{B}

Zygia cataractae (Kunth.) L. Rico) were collected directly from the trees in December 2006 (because these are not deciduous species), air-dried, and stored until needed. Initial concentrations of N, P, total phenols (Graça et al. 2005), and lignin (Goering and Van Soest 1970) were used to characterize the initial chemical quality of the litter (Table 2). Initial leaf toughness was measured in 3 to 4 leaves with a penetrometer (Graça et al. 2005) after leaves had been soaked in distilled water for 1 h. The mass required to force a 0.49- or 1.89-mm^2 iron rod through a leaf immobilized between 2 acrylic sheets was corrected for the rod area, and results were expressed as pressure (g/mm^2) (Table 2). The 3 litter species in each country were chosen to include a slow-, medium-, and fast-decaying species (anticipated from initial litter characteristics). Air-dried leaves were distributed into fine-mesh bags (FM, 20 × 15 cm, 0.5-mm mesh) that prevented entrance of macroinvertebrates and coarse-mesh bags (CM, 20 × 15 cm, 10-mm mesh) that allowed entrance of macroinvertebrates, so that each litter bag contained 3 g of leaves, divided evenly among component species in mixtures. Litter bags were deployed in the temperate stream on 8 January 2007 and in the tropical stream on 15 March 2007. On the same day (day 0), 4 extra litter bags prepared for each litter treatment were taken to the field and returned to the laboratory to be used to calculate the air-dry mass to ash-free dry mass (AFDM) conversion factor, taking into account mass loss from handling. Seven litter treatments (covering 3 richness levels) were used in each stream: A, C, Q, AC, AQ, CQ, and ACQ in Portugal, and I, T, Z, IT, IZ, TZ, and ITZ in Ecuador (Table 3). *Alnus glutinosa* leaves collected in Portugal also were incubated in the tropical stream to help us understand the mechanisms that govern litter processing in both systems (Table 3). Litterbags (n = 3–5) were sampled after 7, 14, 28, 56, and 70 (Portugal) or 94 (Ecuador) d incubation in water. Litter bags were placed in individual Ziploc® bags and kept on ice until processed. In the laboratory, leaves were rinsed gently with distilled water and separated by species from the multispecies litterbags, as suggested by Ostrofsky (2007). Processing component litter species from mixtures individually allowed us to assess the effect of litter richness on the decomposition of individual litter species. Two (Ecuador) or 3 (Portugal) sets of six 12-mm-diameter litter discs cut with a cork borer from litter from fine-mesh bags were used to measure microbial variables

TABLE 3. Summary table of all litter treatments used in the litter decomposition experiment in the temperate deciduous forest and tropical rainforest streams.

Treatment	Temperate stream	Tropical stream
Between streams		
Single species	*Alnus glutinosa* (A)	*Alnus glutinosa* (A)
Within streams: litter mixtures effect		
Single species	*Alnus glutinosa* (A)	*Inga punctata* (I)
	Castanea sativa (C)	*Triplaris dugandii* (T)
	Quercus robur (Q)	*Zygia cataractae* (Z)
2-species mixtures	AC	IT
	AQ	IZ
	CQ	TZ
3-species mixtures	ACQ	ITZ

TABLE 4. Summary table of all measurements made in the litter decomposition experiment in the temperate deciduous forest (temp) and tropical rainforest streams. Mass remaining and all microbial and invertebrate variables were measured on all sampling dates.

		Coarse mesh		Fine mesh	
Litter associated variables	Initial individual litter species	Litter mixture	Individual litter species	Litter mixture	Individual litter species
Litter chemistry	Both				
Litter toughness	Both				
Litter decomposition		Both	Both	Both	Both
Microbial respiration[a]					Temp
Fungal biomass[b]				Both	
Conidial production					Both
Fungal richness					Both
Shredder abundance		Both			
Shredder richness		Both			

[a] Microbial respiration not done in the tropical stream because of logistical constraints
[b] Fungal biomass not measured for individual litter species because of financial constraints

(see below). Litter from coarse-mesh bags was used to evaluate associated macroinvertebrates (see below). Remaining litter from coarse- and fine-mesh bags was oven-dried at 50°C for 48 h, weighed, ignited at 500°C for 4 h and reweighed to calculate the ash fraction and remaining AFDM (Table 4).

Microbial respiration

Microbial O_2 consumption rate was used as a measure of overall microbial activity. O_2 consumption was measured for each litter species incubated alone and in mixtures only in the temperate stream because logistical constraints prevented its measurement in the tropical stream. Measurements were made the day after the bags were collected on a set of 6 litter discs per species per bag in a flow-through system (Graça et al. 2005) set at 15°C. A peristaltic pump with adjustable flow (flow rate: 7.3 ± 2.4 mL/h; mean ±1 SD) was equipped with Watson–Marlow orange/green tubes (Watson–Marlow Pumps Group, Wilmington, Massachusetts). One end of each tube was connected to a respiration chamber (8-mL glass syringes, protected from light) containing 6 litter discs, and the other end entered a reservoir containing 100%-oxygenated distilled water. O_2 saturation was achieved by pumping air into the water through air stones. O_2 concentrations were measured only after the chamber's volume was totally replaced. Water flowing through the chamber was collected with a 1-mL syringe and injected into a 0.1-mL microchamber adapted to an O_2 electrode (Strathkelvin Instruments, Glasgow, Scotland), and readings were made after 30 s. After 3 measurements, flow rate was determined over 20 min with 5-mL calibrated glass vials. AFDM of the litter discs was determined as for the bulk litter (see above), and results were expressed as mg O_2 g^{-1} AFDM h^{-1}.

Fungal biomass

Ergosterol concentrations, used as a measure of fungal biomass (Gessner and Chauvet 1993), were estimated for each litter treatment in both streams. Ergosterol concentration was the only microbial variable that was measured per sample rather than per species within samples. For multispecies samples, 6 litter discs/bag were cut proportionally to the initial litter species mass in the sample. Discs were frozen at −20°C until ergosterol extraction. Discs were freeze-dried, weighed just before extraction, and refluxed in KOH/methanol (8 g/L) in a water bath (80°C) for 30 min. The lipid extract was purified by solid-phase extraction (Waters Sep-Pak® Vac RC tC_{18} cartridges; Waters Corp., Milford, Massachusetts) and quantified by high-performance liquid chromatography (HPLC) by measuring absorbance at 282 nm (Graça et al. 2005). The HPLC system (Dionex, Sunnyvale, California) was equipped with the LiChroCART 250-4 LiChrospher 100 RP-18 (5 µm) column (Merck, Darmstadt, Germany) maintained at 33°C. The mobile phase was 100% methanol, and the flow rate was set at 1.4 mL/min. Ergosterol extraction from all samples was done in Portugal, and fungal biomass was expressed as µg ergosterol/g AFDM.

Conidial production by aquatic hyphomycetes

Conidial production by aquatic hyphomycetes was induced for each litter species incubated alone and in mixtures for both streams. One set of 6 litter discs per species per bag was incubated in a 100-mL Erlenmeyer

flask with 25 mL of distilled water on a shaker (100 rpm) for 48 h at 15 (Portugal) or 25°C (Ecuador). The conidial suspension was transferred to a flask and fixed with 2 mL of 37% formalin for later counting and identification. When preparing slides, 100 µL of Triton X-100 solution (0.5%; Sigma-Aldrich Co., St. Louis, Missouri) was added to the suspension and stirred to ensure an even distribution of conidia. An aliquot of the suspension was filtered (SMWP membrane filters, pore size = 5 µm; Millipore Corp., Bedford, Massachusetts). The filter was stained with 0.05% cotton blue in lactic acid (60%), and spores were identified and counted under a compound microscope at 200× magnification (Graça et al. 2005). AFDM of the litter discs was determined as for the bulk litter (see above). Conidia counting and identification for all samples were done in Portugal, and sporulation rates were expressed as number of conidia mg^{-1} AFDM d^{-1}.

Litter macroinvertebrates

Litter from coarse mesh bags was rinsed into a sieve with 0.5-mm mesh to retain adhering macroinvertebrates. Invertebrates were collected and stored in 90% ethanol. Identification was carried out under a stereomicroscope, generally to genus or species level (except for Oligochaeta [family] and Diptera [family, subfamily or tribe]) with keys published by Tachet et al. (2000) for Portugal and Fernández and Domínguez (2001) for Ecuador. Invertebrates were classified into 2 groups: shredders and nonshredders based on information published by Tachet et al. (2000) for Portugal and Tomanova et al. (2006, 2007), Cheshire et al. (2005), and Merritt and Cummins (1996) for Ecuador. Only shredders were used for statistical analysis.

Data treatment

Comparisons between temperate and tropical streams.— Mass of *Alnus* litter remaining over time in the temperate and tropical streams was used to compute the decomposition rates per day (k/d) by linear regression of ln(x)-transformed data vs time (negative exponential model: $M_r = M_i e^{-kt}$, where M_i is the initial mass, M_r is the remaining mass at time t (d), and k is the decomposition rate). A free intercept was allowed, but intercepts did not differ significantly from 0. Decomposition rates also were calculated per degree day (k/dd) by substituting cumulative mean daily temperature (°C) on the sampling dates for time in the model above to account for differences in water temperature between streams. Analysis of covariance (ANCOVA) was used to compare decomposition of *Alnus* between streams (stream and mesh size as categorical variables, time or dd as the continuous variable). t-tests were used to compare biotic variables (peak values) associated with *Alnus* litter between temperate and tropical streams.

Comparisons within streams: litter-mixture effects.— Mass remaining over time in the temperate stream was used to compute the decomposition rates (k/d) for each litter species incubated alone and in mixtures for each litter treatment. Decomposition rates of each litter species, within each mesh size, were compared among litter treatments by ANCOVA (treatments as the categorical variable, time as the continuous variable) to test whether decomposition rates of individual litter species were affected by the litter richness or composition of the mixture (Ostrofsky 2007). Mass remaining over time for most treatments in the tropical stream did not follow either an exponential- or a linear-decay model. Therefore, decomposition rates could not be calculated accurately in the same way as for the temperate stream. Instead, comparisons among litter species incubated alone and in mixtures and among litter treatments were done by 1-way analysis of variance (ANOVA) applied to the mass remaining on the last sampling date. Decomposition rates (temperate stream) or mass remaining (tropical stream) for each litter species were regressed against litter richness (linear regression) to assess the relationship between decomposition rates/mass remaining of individual litter species and richness of the mixture of their provenance. Decomposition rates/mass remaining of the 7 litter treatments (entire samples) in each stream were regressed against litter richness (linear regression) to assess the overall relationship between decomposition rates/mass remaining of litter mixtures and their richness.

Initial litter chemistry and toughness were compared among litter species, within each system, by 1-way ANOVA. Initial concentrations of N, P, lignin, and total phenols in mixtures were calculated from their concentrations in the component litter species and its initial mass in the mixtures. Decomposition rates/remaining mass of the 7 litter treatments (entire samples) in each stream were regressed against initial litter variables (linear regression) to test for a relationship between litter quality and decomposition rates/remaining mass of litter treatments.

Microbial respiration, conidial production, and species richness of aquatic hyphomycetes associated with each litter species were compared among litter treatments with 2-way ANOVAs (time and litter treatments as the categorical variables; Zar 1999) to test if the biota associated with individual litter species was affected by the litter richness or composition of the mixture from which it was derived.

TABLE 5. Mean (±1 SE) decomposition rates; maximum fungal biomass, conidial production, and fungal richness; shredder abundance; and shredder richness of *Alnus* litter incubated in the temperate deciduous forest and tropical rainforest streams. Time intervals for decomposition rate calculation and time of peak values for fungal and invertebrate variables are also given. AFDM = ash-free dry mass, dd = degree day.

	Temperate stream		Tropical stream	
Litter associated variables	Day(s)	Mean ± SE	Day(s)	Mean ± SE
Decomposition rate (k/d) on coarse-mesh bags	0–70	0.0467 ± 0.0056	0–94	0.0327 ± 0.0069
Decomposition rate (k/d) on fine-mesh bags	0–70	0.0169 ± 0.0027	0–94	0.0060 ± 0.0008
Decomposition rate (k/dd) on coarse-mesh bags	0–70	0.0055 ± 0.0006	0–94	0.0014 ± 0.0003
Decomposition rate (k/dd) on fine-mesh bags	0–70	0.0020 ± 0.0003	0–94	0.0002 ± <0.0001
Fungal biomass (μg ergosterol/g AFDM)	14	838 ± 228	14	303 ± 34
Conidial production (no. conidia mg^{-1} AFDM d^{-1})	14	3261 ± 2342	28	14 ± 13
Fungal richness (no. taxa/bag)	28	9 ± 1	28	1 ± 0
Shredder abundance (no. individuals/g AFDM)	70	39 ± 34	28	31 ± 11
Shredder richness (no. taxa/bag)	28	4 ± 0	28	3 ± 1

Cumulative conidial production by the end of the experiment was calculated by summing the values of daily production on each sampling date and linearly interpolating values for each day between sampling dates. The percentage of initial litter AFDM of each litter treatment converted into conidia was calculated after multiplying the cumulative conidial production at the end of the experiment by the mean mass of 1 conidium (obtained from the literature; Bärlocher and Schweizer 1983, Chauvet and Suberkropp 1998), and was regressed against litter richness (linear regression).

Fungal biomass and the abundance and richness of shredders were not measured for each litter species individually but for each litter treatment. These variables were compared among litter treatments by 2-way ANOVAs (time and litter treatment as the categorical variables).

Data were transformed ($\log[x]$ or $\log[x + 1]$) when necessary to achieve normality (Shapiro–Wilks test) and homoscedasticity (Bartlett χ^2 test) (Zar 1999). Tukey's Honestly Significant Difference test was used for multiple comparisons when necessary. Statistical analyses were done with Statistica software (version 6.0; StatSoft, Tulsa, Oklahoma).

Results

Comparisons between temperate deciduous forest and tropical rainforest streams

Alnus litter decomposition proceeded at similar rates in both streams (k_{CM} = 0.0467/d and 0.0327/d, k_{FM} = 0.0169/d and 0.0060/d, in the temperate and tropical streams, respectively; ANCOVA, $p = 0.985$) and was significantly faster in the coarse-mesh than in the fine-mesh bags ($p < 0.001$). However, when decomposition rates were corrected for temperature, mass loss was much faster in the temperate than in the tropical stream (k_{CM} = 0.0055/dd and 0.0014/dd, k_{FM} = 0.0020/dd and 0.0002/dd, respectively; ANCOVA, $p = 0.012$) and faster in the coarse-mesh than in the fine-mesh bags ($p < 0.001$) (Table 5).

Alnus litter supported less fungal biomass, less conidial production, and fewer fungal species in the tropical stream (maxima: 303 μg ergosterol/g AFDM, 14 conidia mg^{-1} AFDM d^{-1}, 1 species/bag, respectively) than in the temperate stream (838 μg ergosterol/g AFDM, 3261 conidia mg^{-1} AFDM d^{-1}, 9 species/bag, respectively) (t-test, $p = 0.004$, 0.008, and 0.001, respectively; Table 5). The abundance and richness of shredders associated with *Alnus* litter were similar between streams (t-test, $p = 0.482$ and 0.582, respectively; Table 5).

Comparisons within streams: litter-mixture effects

Litter decomposition.—In general, decomposition of constituent species in litter mixtures was not affected by the number of species in the mixture (Fig. 1A–D). In the temperate stream, the decomposition rate of *Alnus* litter incubated in coarse-mesh bags differed among litter treatments (Fig. 1A). *Alnus* from the 3-species mixture decomposed faster than *Alnus* incubated alone or in the 2-species mixtures (ANCOVA, $p < 0.034$). This difference resulted in a significant and positive relationship between *Alnus* decomposition rates and species richness (linear regression, $R^2 = 0.96$, $p = 0.022$). The decomposition rate of *Castanea* litter in fine-mesh bags also differed among treatments (Fig. 1B). Litter incubated in the presence of *Alnus* decomposed faster than litter incubated alone or in the 3-species mixture (ANCOVA, $p < 0.034$). No significant differences in mass remaining were found in the tropical stream (Fig. 1C, D).

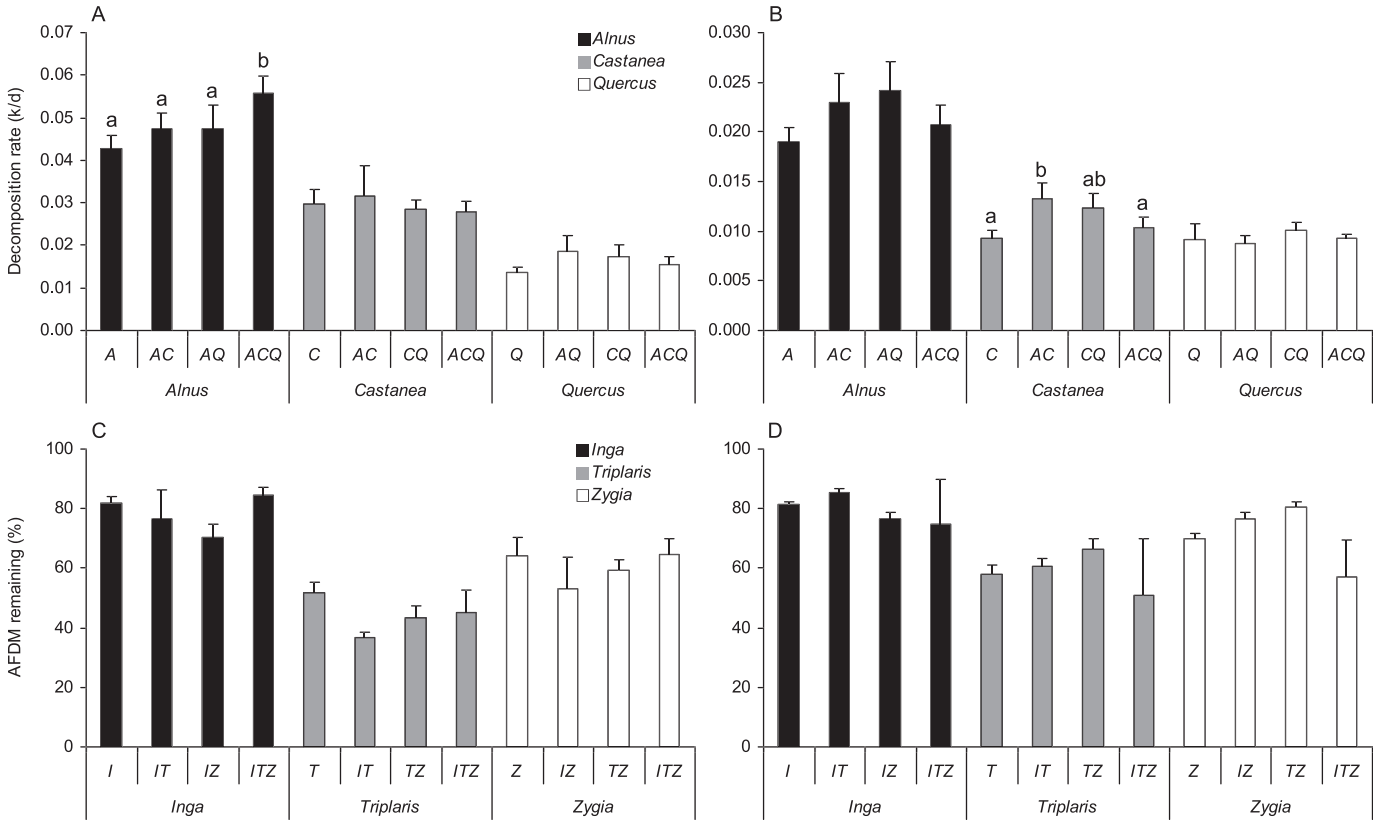

FIG. 1. Mean (+1 SE) decomposition rates (temperate deciduous forest stream) (A, B) and mass remaining (tropical rainforest stream) (C, D) of individual litter species derived from single- and mixed-species in coarse (A, C) and in fine-mesh (B, D) litter bags. Bars with the same letter are not significantly different (Tukey's test, $p > 0.050$). A = *Alnus*, C = *Castanea*, Q = *Quercus*, I = *Inga*, T = *Triplaris*, Z = *Zygia*.

Decomposition rate of litter mixtures was not related to litter species richness in bags of either mesh size or in either stream (linear regressions, $p > 0.664$). In the temperate stream, decomposition rates of the 7 litter treatments were positively related to initial N (linear regression, coarse-mesh bags: $R^2 = 0.74$, $p = 0.013$, fine-mesh bags: $R^2 = 0.92$, $p = 0.001$) and lignin concentrations (coarse-mesh bags: $R^2 = 0.73$, $p = 0.014$) and negatively related to P concentrations (coarse-mesh bags: $R^2 = 0.65$, $p = 0.027$) and initial polyphenol (coarse-mesh bags: $R^2 = 0.80$, $p = 0.006$) (Fig. 2A–D). Polyphenol concentrations were positively related to P (linear regression, $R^2 = 0.97$, $p < 0.001$) and negatively related to lignin ($R^2 = 0.99$, $p < 0.001$). In the tropical stream, the % mass remaining of the 7 litter treatments was positively related to the initial lignin concentration (linear regression, coarse-mesh bags: $R^2 = 0.57$, $p = 0.050$).

Microbial respiration.—The microbial O_2 consumption rate for *Alnus* litter derived from single- and mixed-species litter bags varied between 0.21 and 0.77 mg O_2 g^{-1} AFDM h^{-1} across litter treatments and time. The respiration rates of *Castanea* ranged from 0.08 to 0.70 mg O_2 g^{-1} AFDM h^{-1}, whereas for *Quercus* the rates ranged from 0.09 to 0.48 mg O_2 g^{-1} AFDM h^{-1}. In all cases, species richness did not affect respiration rates (2-way ANOVA, $p > 0.061$; Table 6).

Fungal biomass.—The litter was already colonized by fungi before deployment in the streams (28–445 µg ergosterol/g AFDM on day 0). Fungal biomass was affected by litter treatment and time in both streams, and the treatment × time interaction in the temperate stream (Table 7). After immersion, fungal biomass dynamics showed opposite trends for litter in the temperate and tropical streams. In the temperate stream, fungal biomass increased over time or, in the case of *Alnus* litter incubated alone, peaked on day 14 (Fig. 3A). Ergosterol differed between *Quercus* and all other treatments (Tukey's HSD, $p < 0.006$) except *Alnus*/*Quercus* ($p = 0.306$), and between *Alnus*/*Quercus* and *Castanea* and *Alnus*/*Castanea* ($p < 0.001$, $p = 0.008$, respectively). Litter treatments with *Quercus* litter tended to have lower fungal biomass (Fig. 3A). In the tropical stream, fungal biomass generally decreased from the first sampling date to the end of the experiment (Fig. 3B). Fungal biomass

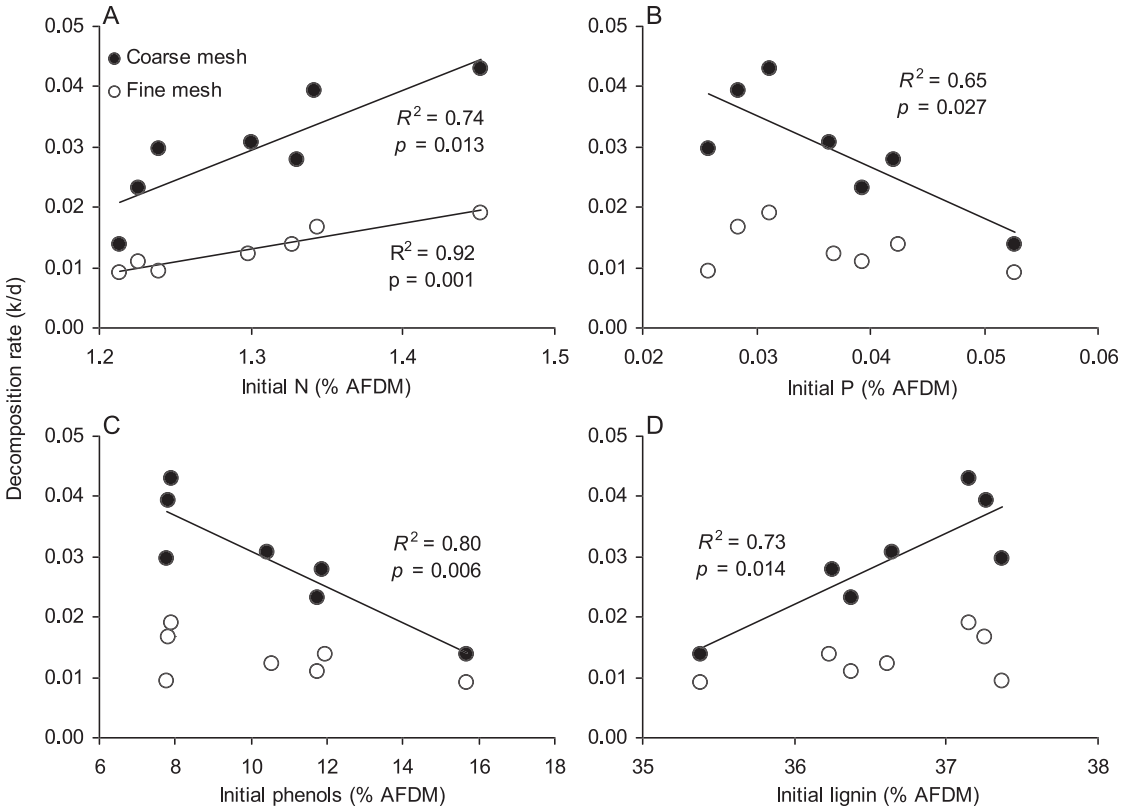

FIG. 2. Relationship between initial % N (A), % P (B), % phenols (C), and % lignin (D) of litter and decomposition rate of litter treatments incubated in the temperate deciduous-forest stream. R^2 and p values are given for significant relationships (linear regression, $p < 0.050$). AFDM = ash-free dry mass.

was lowest on *Triplaris* litter (Tukey's HSD, $p < 0.002$; Fig. 3B).

Conidial production by aquatic hyphomycetes.—Conidial production in the temperate stream changed over time and differed among litter treatments (Table 6). Conidial production generally peaked by day 14 (maximum values in *Alnus*, *Castanea*, and *Quercus* litter of 1580–4505, 1337–2378, and 833–2886 conidia mg^{-1} AFDM d^{-1}, respectively; Fig. 4A–C). Sporulation rates were affected by litter treatment only in *Castanea* litter (Table 6) and were lower in *Castanea* litter incubated with *Alnus* than in *Castanea* litter incubated in the 3-species mixture (Tukey's HSD, $p = 0.040$). The kinetics of fungal species richness was similar among treatments for all species (2-way ANOVA, $p > 0.159$), and increased to a peak of 7 to 9 species between days 28 and 56. In the tropical stream, conidial production was very low. A peak generally was reached by day 14 (20–167 conidia mg^{-1} AFDM d^{-1} across species and treatments) and fell to 0 soon after, so 40% of samples had no conidia (Fig. 4D–F). The mean number of species/sample was typically <1, precluding reliable statistical comparison among treatments.

The % initial litter converted into conidia varied between 4.66 and 18.57% across species and treatments in the temperate stream and between 0.04 and 2.28% in the tropical stream. The % initial litter converted into conidia was positively and significantly related to litter richness only in the temperate stream (linear regression, $R^2 = 0.53$, $p = 0.007$).

Macroinvertebrates in the litter.—In the temperate stream, the most common shredders were stoneflies of the families Leuctridae and Nemouridae and the caddisfly *Allogamus laureatus* (Limnephilidae). Shredder abundance and richness differed among litter treatments in both streams (Table 7). Shredder abundance was significantly higher in *Alnus* litter (the softest species) than in *Quercus* or in the 3-species mixture (Tukey's HSD, $p < 0.019$, $p < 0.013$, respectively; Fig. 5A). Shredder richness followed a similar pattern but was significantly higher in *Alnus* than in the 3-species mixture in the temperate stream (Tukey's HSD, $p = 0.021$; Fig. 5B). In the tropical stream, the most common shredders were the mayflies *Caenis* sp. (Caenidae), *Miroculis* sp., *Fittkaulus* sp., and *Ulmeritoides* sp. (Leptophlebiidae), and Chironomid midges. Shredder abundance was significantly higher in

TABLE 6. Summary table for 2-way analyses of variance done on microbial respiration, conidial production, and species richness of aquatic hyphomycetes associated with individual litter species derived from single- and mixed-species litter bags (treatment) incubated in the temperate deciduous forest stream.

	Alnus			*Castanea*			*Quercus*		
Source	df	*F*	*p*	df	*F*	*p*	df	*F*	*p*
Microbial respiration									
Litter treatment	3	0.576	0.636	3	2.677	0.061	3	0.674	0.573
Time	2	1.700	0.204	4	6.142	0.001	4	9.502	<0.001
Litter treatment × time	6	1.187	0.347	12	0.655	0.782	12	0.654	0.782
Conidial production by aquatic hyphomycetes[a]									
Litter treatment	3	2.211	0.108	3	3.931	0.015	3	2.185	0.106
Time	3	29.886	<0.001	4	33.464	<0.001	4	78.695	<0.001
Litter treatment × time	9	1.957	0.083	12	2.105	0.040	12	0.707	0.735
Aquatic hyphomycete species richness[a]									
Litter treatment	3	0.322	0.809	3	1.821	0.159	3	1.259	0.302
Time	3	21.399	<0.001	4	37.182	<0.001	4	48.816	<0.001
Litter treatment × time	9	1.848	0.102	12	0.525	0.885	12	2.631	0.012

[a] $\log(x + 1)$-transformed

Triplaris litter (the softest species) than in *Zygia* or in *Inga/Zygia* (Tukey's HSD, $p < 0.021$, $p < 0.026$, respectively; Fig. 5C), and shredder richness was higher in *Triplaris* than in *Zygia* ($p = 0.043$; Fig. 5D).

Discussion

Comparisons between temperate deciduous forest and tropical rainforest streams

Litter decomposition varied greatly between the temperate and tropical streams. Litter decomposed faster in the temperate stream than in the tropical stream in spite of the higher water temperature in the tropics. This result is consistent with those of other studies in which tropical and temperate streams were compared (Gonçalves et al. 2006, 2007), but contrary to the pattern suggested by the metabolic rate theory (Brown et al. 2004).

In the temperate stream, fungal biomass increased over time, or until it reached a peak, as usually described in the literature (Gessner and Chauvet 1994), whereas in the tropical stream it decreased, indicating fungal disappearance. The terrestrial fungi colonizing the litter before submersion, revealed by

TABLE 7. Summary table for 2-way analyses of variance done on fungal biomass and shredder abundance and species richness associated with litter treatments incubated in the temperate deciduous forest and tropical rainforest streams.

	Temperate stream			Tropical stream		
Source	df	*F*	*p*	df	*F*	*p*
Fungal biomass[a]						
Litter treatment	6	9.031	<0.001	6	8.376	<0.001
Time	5	95.097	<0.001	4	3.523	0.011
Litter treatment × time	30	3.690	<0.001	24	1.154	0.315
Shredder abundance[b]						
Litter treatment	6	3.743	0.002	6	3.875	0.002
Time	4	2.950	0.025	4	12.374	<0.001
Litter treatment × time	24	0.780	0.751	24	0.684	0.857
Shredder richness[b]						
Litter treatment	6	2.709	0.019	6	3.165	0.007
Time	4	13.117	<0.001	4	15.848	<0.001
Litter treatment × time	24	1.461	0.105	24	0.646	0.890

[a] $\log(x)$-transformed
[b] $\log(x + 1)$-transformed

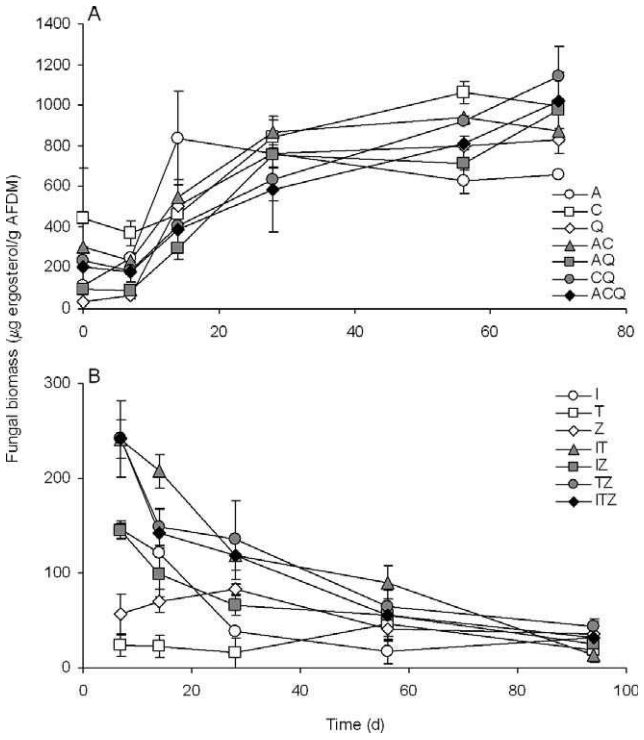

FIG. 3. Mean (±1 SE) fungal biomass associated with litter treatments incubated in the temperate deciduous forest (A) and tropical rainforest (B) streams. Fungal biomass was determined from the mixtures and not from component litter species. A = *Alnus*, C = *Castanea*, Q = *Quercus*, I = *Inga*, T = *Triplaris*, Z = *Zygia*. AFDM = ash-free dry mass.

the initial ergosterol concentrations, could have been progressively replaced by their aquatic counterparts in the temperate stream. This replacement was not observed in the tropical stream, probably because of extremely low conidial density in the water column (VF, personal observation), which might, in turn, be explained by environmental conditions in the stream water (Table 1). Similarly, conidial production by aquatic hyphomycetes was up to 2 orders of magnitude higher in the temperate than in the tropical rainforest stream, which further indicates that aquatic hyphomycetes had a minor role in litter decomposition in the tropical stream, when compared with the temperate one. These results resemble those of studies in the Brazilian Cerrado and montane Andean forests in Ecuador, where reproductive activity of aquatic hyphomycetes was very low (Gonçalves et al. 2007, Encalada et al. 2010).

The lower decomposition rate in the rainforest stream can be explained by the low fungal biomass. The reasons for these differences in fungal biomass between systems are beyond the scope of our study, but they may be related to unfavorable conditions, such as high water temperature, low dissolved O_2, and low current speed, in the tropical rainforest stream. Aquatic hyphomycetes prefer cool, well aerated, flowing waters (Bärlocher 1992). The Amazonian stream in our study is subject to drastic fluctuations in hydrology, as have been seen in other Amazonian waters (Rueda-Delgado et al. 2006), which might lead to changes in chemical and physical variables (Leite et al. 2011). Specifically, Leite et al. (2011) reported a strong intra-annual relationship between discharge and pH values, with low pH values at higher discharge. Short-term acidification of stream water associated with these fluctuations (McClain and Elsenbeer 2001) might further limit microbial diversity and activity (Mulholland et al. 1987, Dangles et al. 2004, Baudoin et al. 2008). Fungal biomass was higher in *Alnus* litter incubated in the tropical stream than in the native tropical species on the first 3 sampling dates, a result indicating that litter quality also might be an important factor modulating fungal colonization of leaf litter. Last, if tropical leaves are strongly protected against consumers (reviewed by Coley and Barone 1996), some unknown defensive compounds could leach into the water and inhibit microbial growth.

The kinetics and magnitude of invertebrate colonization of submerged litter were comparable between streams. This result supports the claim that the abundance of invertebrates, and shredders in particular, in some tropical streams is at the level found in temperate streams (Cheshire et al. 2005, Encalada et al. 2010). However, if we consider the decomposition ratio between coarse-mesh (overall decomposition) and fine-mesh bags (microbial decomposition), invertebrate feeding activity was clearly higher in the temperate (k_{CM}/k_{FM} = 1.5–3.2) than in the tropical stream (mass loss_{CM}/mass loss_{FM} = 0.8–2.1). This difference might have resulted from lower colonization of litter by aquatic hyphomycetes and tougher leaves in the tropical stream (Graça et al. 2001, Graça and Cressa 2010). The difference between mesh sizes was especially evident for the softer litter species (*Alnus*, *Castanea*, and *Triplaris*), results supporting the suggestion that toughness is a determinant litter characteristic for invertebrate feeding as suggested by Graça and Cressa (2010). Physical abrasion probably was a secondary factor affecting litter decomposition in both streams because current velocity was within the values reported by Ferreira et al. (2006a) as contributing little to mass loss.

Comparisons within streams: litter-mixture effects

Regardless of the differences in processing rate between the 2 systems, no consistent relationship was

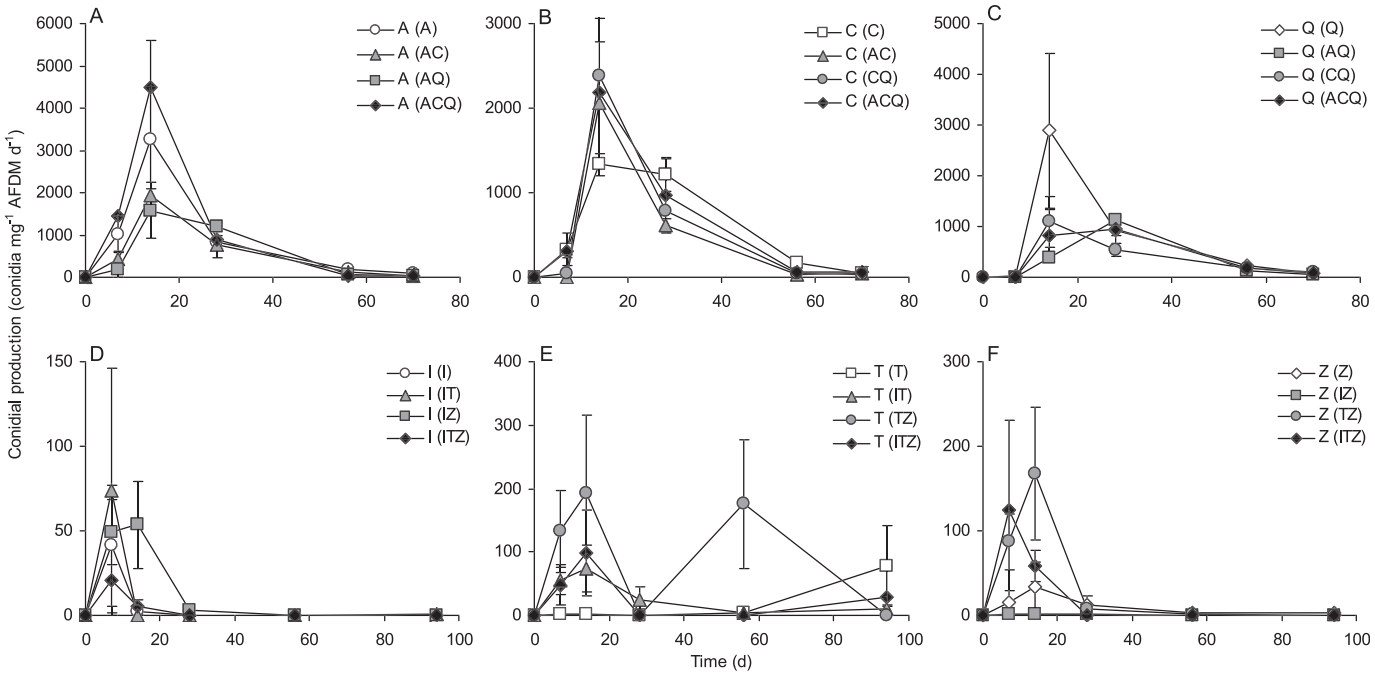

FIG. 4. Mean (±1 SE) conidial production associated with *Alnus* (A) (A), *Castanea* (C) (B), and *Quercus* (Q) (C) derived from single- and mixed-species litter bags incubated in the temperate deciduous forest and *Inga* (I) (D), *Triplaris* (T) (E), and *Zygia* (Z) (F) derived from single- and mixed-species litter bags incubated in the tropical rainforest streams.

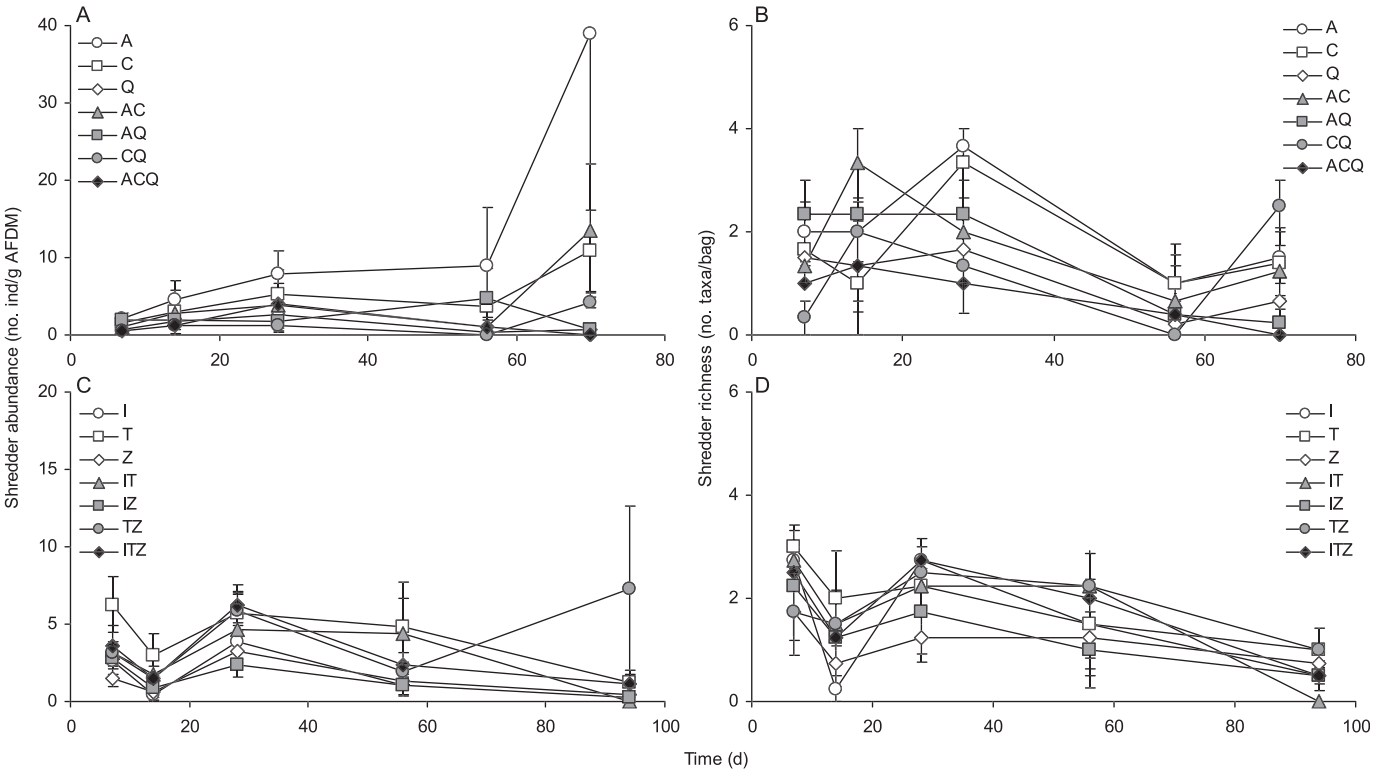

FIG. 5. Mean (±1 SE) shredder abundance (A, C) and richness (B, D) associated with litter treatments incubated in the temperate deciduous forest (A, B) and tropical rainforest (C, D) streams. A = *Alnus*, C = *Castanea*, Q = *Quercus*, I = *Inga*, T = *Triplaris*, Z = *Zygia*. AFDM = ash-free dry mass.

observed between decomposition of litter mixtures and litter species richness in either the temperate or the tropical stream. These results suggest that litter species richness may not be an important factor affecting decomposition of diverse litter packs, at least at the low richness levels used in our study (Swan and Palmer 2004, Lecerf et al. 2007b, but see Kominoski et al. 2007). However, litter decomposition was sensitive to litter identity/quality, especially in the temperate stream where the presence of *Alnus* in litter packs stimulated mass loss and the presence of *Quercus* tended to slow mass loss. Others have demonstrated the importance of the identity/quality of companion litter species for individual litter decomposition when litter types with contrasting chemical characteristics were mixed (Abelho 2009, Sanpera-Calbet et al. 2009).

The strong relationship between litter decomposition and initial N and phenol concentrations in the temperate stream and initial lignin concentration in the tropical stream suggested that decomposition of litter also was related to initial chemical composition. These results are consistent with the literature (Gessner and Chauvet 1994, Lecerf et al. 2007b, Schindler and Gessner 2009). The relationship between litter quality and decomposition was especially evident for coarse-mesh bags, a result suggesting that the relationship was mediated by invertebrates (see below). These results agree with those of many related studies in which litter identity (i.e., biological traits and chemical composition) was more important than species richness in decomposition of litter mixtures (Moore and Fairweather 2006, Swan and Palmer 2006, Lecerf et al. 2007b, Abelho 2009, Schindler and Gessner 2009).

The apparent absence of an effect of litter richness on decomposition could arise if the decomposition of component litter species in a mixture were affected in opposite ways (an overall null effect) or if litter mixing had no effect on decomposition of any component species. For instance, in the temperate stream, the difference in decomposition rate between *Alnus* and *Quercus* in coarse-mesh bags tended to decrease when they were incubated together ($k_{A(A)}/k_{Q(Q)} = 3.1$, $k_{A(AQ)}/k_{Q(AQ)} = 2.6$) because decomposition rate of *Quercus* increased in the presence of *Alnus*. In the tropical stream, the difference in decomposition rates between *Zygia* and *Inga* in coarse- and fine-mesh bags tended to decrease when they were incubated together (mass $\text{loss}_{Z(Z)}$/mass $\text{loss}_{I(I)} = 2.0$ in coarse mesh and 1.6 in fine mesh, mass $\text{loss}_{Z(IZ)}$/mass $\text{loss}_{I(IZ)} = 1.7$ and 1.1) because *Zygia* stimulated decomposition of *Inga*. In the litter mixtures, N-poor species (*Quercus*, *Inga*) could have benefited from nutrient transfer from N-rich species (*Alnus*, *Zygia*), enhancing microbial activity on the nutrient-poor species (Liu et al. 2007, Taylor et al. 2007, Xiang and Bauhus 2007). *Alnus* could have attracted detritivores that would feed on *Quercus* litter, whereas decomposers and detritivores might have preferred the soft *Inga* litter with low phenolic concentration to the tough, phenol-rich *Zygia* (Gonçalves and Canhoto 2009). Thus, some litter traits (e.g., chemical composition) may affect adjacent species in the mixture.

Nevertheless, the sensitivity of the nutrient-rich *Alnus* to litter richness was surprising given that it was the fastest-decomposing species in monoculture. However, in the presence of less nutritive litter in the 2- and 3-species mixtures, *Alnus* might have been consumed preferably by invertebrates. When able to choose, invertebrates prefer the litter that is richer in nutrients (Canhoto and Graça 1995, Graça et al. 2001, Gonçalves and Canhoto 2009, Graça and Cressa 2010). Therefore, decomposition of component litter species in mixtures appears to depend more on the identity than on the number of companion species, and the effect of species richness on component species appears to depend on the identity of the component species.

Microbial O_2 consumption, a measure of overall microbial activity, was not related to species richness or species composition. More time might have been needed for differences in respiration/metabolism of fungi on different species of litter to appear. However, lack of power to measure differences cannot be ruled out, given methodological constraints and high variability among values.

Neither fungal biomass nor sporulation rates were affected by litter species richness in either stream. However, in the temperate stream, *Quercus* seemed to be a key species during the first stages of decomposition because its presence limited accumulation of fungal biomass. The effect of certain litter species on accumulation of fungal biomass has been described by Kominoski et al. (2007) and Sanpera-Calbet et al. (2009). In our study, the negative effect of *Quercus* might be attributable to its greater toughness and phenolic concentration, both of which negatively affect microbial colonization (Canhoto and Graça 1996, Quinn et al. 2000). However, the amount of litter mass converted into conidia was positively and significantly related to litter richness in the temperate stream, a result that might suggest resource complementarity. Here again, litter identity seems to be important for fungal biomass accrual.

Invertebrate abundance and species richness generally were not affected by litter richness, although the identity of litter species seemed to affect colonization

of litter by invertebrates. In the temperate stream, litter mixtures with tough *Quercus* litter had lower abundance and richness of invertebrates than mixtures without *Quercus*. This difference led to a tendency for litter treatments without *Quercus* to decompose faster than treatments with *Quercus* in coarse-mesh bags (exposed to invertebrate activity). In the tropical stream, mixtures with soft *Triplaris* litter had higher invertebrate abundance and richness than mixtures without *Triplaris*. This result indicates that invertebrates colonized litter for feeding and not only for protection because they would have been more abundant in treatments where the tougher litter was present if protection were important (Kominoski and Pringle 2009, Sanpera-Calbet et al. 2009).

Our results should be interpreted with caution because litter diversity was manipulated only inside litter bags, and the biotic community might have been under the general influence of litter diversity/quality of the surrounding environment. Changes in litter diversity might affect litter decomposition and associated biological colonization directly (as addressed in our study), but also through changes in the decomposition environment. Despite this possibility, litter bags have been the approach most often used to address the litter diversity–litter decomposition relationship. A few investigators have manipulated litter diversity in the environment in terrestrial systems (Hector et al. 2000, Hobie et al. 2006, Miyamoto and Hiura 2007). Implementation of such an experiment in small woodland streams would be challenging because of the unidirectional flow downstream and the predominantly longitudinal dimension and associated spatial heterogeneity of small streams. However, such experiments would allow greater certainty when scaling up results.

Concluding remarks

Our study was carried out in 2 streams in contrasting systems. Lower litter mass loss in the tropical rainforest stream could be attributed to unfavorable environmental conditions (high temperature, low dissolved O_2, low current velocity, and unstable water chemistry), which impaired fungal activity and growth. Low fungal activity can result in low litter quality for shredders, thereby impairing invertebrate feeding activities. Nevertheless, litter decomposition responded similarly to manipulation of species richness and identity even though the streams differed greatly in environmental conditions. Overall, our results indicate that decomposition of litter in mixtures might differ from its decomposition when incubated alone depending on the identity (quality) of the companion and the target litter species. The effects of litter quality on litter decomposition were reinforced mainly by invertebrate activity. These results have strong implications at several levels. For instance, calculations of C budgets for freshwaters—which acquire increased relevance under a global-warming scenario or under vegetation changes along the riparian zones—usually are based on decomposition rates of litter species when they are decomposing alone (Buzby and Perry 2000, Webster et al. 2001, Molinero and Pozo 2006). However, litter packs in streams are usually multispecies compositions (Swan and Palmer 2004, Bastian et al. 2007, Swan et al. 2009), so ideally, calculations of C budgets should take into consideration estimates of decomposition rates derived from litter mixtures. Litter quality is expected to decrease in a CO_2-enriched atmosphere (Stiling and Cornelissen 2007), and quality is an important predictor of decomposition of litter in mixtures. Thus, decomposition rates determined under the present conditions might not allow precise forecasting of decomposition rates in the future, even if mixtures consist of the same species combination (Hoorens et al. 2002). Moreover, certain litter species (*Alnus*, *Quercus*) seem to drive the decomposition of the litter packs where they are present, which might have important ecological consequences if these key species disappear. In Europe, *Alnus* trees are becoming infested by the fungus *Phytophthora alni* (Thoirain et al. 2007, Brasier et al. 2008), which rapidly kills contaminated trees. The disappearance of *Alnus* trees from stream banks could reduce instream litter decomposition directly because *Alnus* is a fast-decomposing species, and indirectly because its presence stimulates decomposition of poor-quality litter. The same consideration applies to the invasion of tropical riparian zones by exotic plants (O'Connor et al. 2000). Changes in riparian species composition, especially if they involve species that take part in the N cycle (e.g., N-fixing riparian trees, such as species in the genera *Alnus* and *Inga*), might affect water chemistry (Shaftel et al. 2012) and, consequently, litter decomposition (Shaftel et al. 2011). No overall relationship was found between decomposition of litter mixtures and litter richness, but ecosystem functioning might still be impaired by the loss of key riparian species, whose role in instream nutrient turnover might not be anticipated.

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