



A Global Assessment of the Effects of Eucalyptus Plantations on Stream Ecosystem Functioning

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ABSTRACT

Forest change is a major environmental problem worldwide. Forest streams, with their large aquatic–terrestrial interface and strong dependence on terrestrially derived organic matter, are highly sensitive to forest changes. Fast-wood plantations can be particularly threatening if they markedly differ from native forests. *Eucalyptus* plantations, in particular, cover large areas worldwide (> 20 million ha, mostly from 35°S to 35°N), but their

effects on stream functioning have been addressed mostly in the Iberian Peninsula, which limits generalization to other regions. We assessed the effect of eucalyptus plantations on total (microbial decomposers and macroinvertebrates; in coarse mesh bags) and microbial-driven (in fine mesh bags) leaf litter decomposition by comparing streams flowing through native forests and eucalyptus plantations in seven regions in the Iberian Peninsula, Central Africa and South America. We found an overall significant inhibition of total litter decomposition by 23%. The effect did not significantly differ across regions, although a significant inhibition was found for Spain (– 41%), South Brazil (– 31%) and Uruguay (– 36%) (Portugal had a marginally nonsignificant inhibition by 50%) but not for other regions, suggesting that the effects of plantations in temperate climates are mediated through effects on macroinvertebrate communities.

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Contrarily, the overall effect for microbial-driven litter decomposition was non-significant, but it significantly differed across regions with a significant stimulation in Central Brazil (110%) and Uruguay (32%), and nonsignificant effects for other regions (Kenya had a marginally nonsignificant inhibition by 48%), suggesting that functional redundancy among microbial communities is not general and effects can occur if plantations induce changes in nutrient availability, solar irradiation or litter characteristics.

Key words: effect size; forest change; leaf litter decomposition; mesh bags; meta-analysis; response ratio; stream functioning.

HIGHLIGHTS

- Effects of eucalyptus plantations on stream functioning were assessed in seven regions.
- Effects of plantations on litter decomposition depended on decomposer communities and region.
- Inhibition of decomposition was mostly mediated by effects on macroinvertebrates.

INTRODUCTION

Total forest area has decreased worldwide, while the area occupied by tree plantations has increased (Payn and others 2015). In 2000, approximately 90 million ha were occupied by large-scale monocultures that are intensively managed to produce high volumes of wood at a fast rate (Gerber 2011). Such plantations are mostly used to supply the paper industry in developing countries and have been promoted for mitigating climate change by trapping atmospheric carbon (Bäckstrand and Lövbrand 2006; Zomer and others 2008). Thus, the increased paper demands and the opportunities created by the carbon sequestration market will likely increase the pace of land conversion into fast-wood plantations.

Eucalyptus plantations occupy large areas worldwide (ca. 20 million ha in 2009; Iglesias-Trabado and Wilstermann 2009), mostly between 35°S and 35°N. In the Iberian Peninsula, these plantations occupy 1.5 million ha (IFN3 2007; ICNF 2013) and are the predominant type of industrial fast-wood plantation in the southern hemisphere (Iglesias-Trabado and Wilstermann 2009). The replacement of native forests by eucalyptus plantations may

strongly affect streams due to their large aquatic-terrestrial interface and strong dependence on riparian litter (Vannote and others 1980; Wallace and others 1997).

Eucalyptus trees have high water demands (Calder 2002), leading to decreases in runoff and in aquifer levels (Lara and others 2009). Also, soils in eucalyptus plantations are highly hydrophobic (Abelho and Graça 1996; Fernández and others 2006), likely due to the accumulation of oils released from the leaves, hindering rain water penetration and the replenishment of groundwater reservoirs. Thus, stream hydrology is generally altered, with reduced water flow over the year, spates during heavy rain events and drought during the dry season, especially in arid regions (Scott and Lesch 1997; Lara and others 2009; Cordero-Rivera and others 2017). Streams flowing through plantations may also have altered light and temperature regimes, if single-stemmed eucalyptus trees replace wide-canopy deciduous trees.

Eucalyptus plantations may also promote changes in stream substrates and habitats due to the deposition of bark and branches (Pozo and others 1997; Molinero and Pozo 2004; Santiago and others 2012) and fine sediments (Siegloch and others 2014). Additionally, streams flowing through eucalyptus plantations may endure changes in litter fall phenology, diversity, quantity and quality when these plantations replace diverse native forests composed of trees with traits markedly different from those of eucalyptus (Abelho and Graça 1996; Pozo and others 1997; Graça and others 2002; Molinero and Pozo 2004, 2006). These changes in environmental characteristics may affect aquatic biota and ecosystem processes, which may jeopardize streams ability to provide ecosystem services (for example, good water quality, food) (Graça and others 2002; Ferreira and others 2016).

One fundamental ecosystem process in forest streams is litter decomposition (Vannote and others 1980; Wallace and others 1997), which is mostly a biological process carried out by microbial decomposers (mostly aquatic hyphomycetes) and macroinvertebrate shredders (Hieber and Gessner 2002). Microbes colonize the litter soon after it has leached secondary compounds with antimicrobial activity (for example, polyphenols), and their activities lead to the mineralization of organic carbon, incorporation of carbon and nutrients into microbial biomass and litter softening (Hieber and Gessner 2002; Gulis and Suberkropp 2003; Gulis and others 2006). These changes increase litter palatability to shredders who incorporate it into

secondary production (Hieber and Gessner 2002; Cornut and others 2010). The relative role of microbes and macroinvertebrates on litter decomposition depends on environmental characteristics with cool-water streams (for example, at higher latitude or elevation) generally bearing higher species richness and density of shredders, which contribute significantly to litter decomposition, than warm-water streams where litter decomposition can be mostly microbial-driven (Dobson and others 2002, 2004; Gonçalves and others 2006; Boyero and others 2011a, b). Litter traits also moderate the role of macroinvertebrates on decomposition since these generally prefer soft and nutrient-rich litter over more recalcitrant litter that is mostly decomposed by microbes (Canhoto and Graça 1995; Hieber and Gessner 2002; Gonçalves and others 2007; Casotti and others 2014; Kiffer and others 2018).

According to a recent meta-analysis, total (that is, macroinvertebrate + microbial-driven) litter decomposition is reduced in streams flowing through eucalyptus plantations compared with streams in native deciduous forests in the Iberian Peninsula (Ferreira and others 2016). This is likely due to the lower taxa richness, density or biomass of benthic macroinvertebrates generally found in the former than the latter streams (Abelho and Graça 1996; Larrañaga and others 2009a, 2009b; Ferreira and others 2015; Cordero-Rivera and others 2017). The same meta-analysis reported that microbial-driven litter decomposition is less affected by forest change than total litter decomposition (Ferreira and others 2016). Although species richness and evenness of aquatic hyphomycetes are generally lower in streams flowing through plantations than in streams in native deciduous forests in Portugal, and community structure differs between stream types in both Portugal and Spain (Chauvet and others 1997; Bärlocher and Graça 2002; Ferreira and others 2006), the weak response of microbial-driven litter decomposition to forest change suggests high functional redundancy in microbial communities between stream types (Bärlocher and Graça 2002; Ferreira and others 2006).

Importantly, however, most studies addressing the effects of eucalyptus plantations on stream functioning have been carried out in the Iberian Peninsula (reviewed by Graça and others 2002; Ferreira and others 2016), which limits generalization to regions with distinct climate, vegetation and contribution of macroinvertebrates to litter decomposition. For instance, it is uncertain what would the effect of eucalyptus plantations be on

litter decomposition in streams in regions with high precipitation and where streams do not dry out (for example, in tropical afro-montane forests), in regions with riparian vegetation dominated by evergreen species with recalcitrant litter (for example, in the Brazilian savannah), or in regions where macroinvertebrates are not important decomposers and litter decomposition is mostly microbial-driven (for example, some tropical regions). Several studies have compared the decomposition of native leaf litter with that of different eucalyptus species (*Eucalyptus globulus*: Canhoto and Graça 1996; *Eucalyptus grandis*: Gonçalves and others 2012a; *Eucalyptus camaldulensis*: Gonçalves and others 2012b; *Eucalyptus cloeziana*: Rezende and others 2014), but these do not allow assessing the full effects of forest change (which go beyond those mediated by changes in litter characteristics) on ecosystem processes.

We present the first global assessment of how litter decomposition is affected by eucalyptus plantations, including seven regions distributed across the Iberian Peninsula, Central Africa and South America. In this collaborative, coordinated study, we tested the following hypotheses: (1) Eucalyptus plantations have an effect on litter decomposition, and the effect depends (2) on the type of decomposer community involved (total: macroinvertebrates + microbes or microbes only), and (3) on the region.

MATERIALS AND METHODS

Study Sites

Three streams flowing through native forests (henceforth, native streams) and three streams flowing through eucalyptus plantations (henceforth, eucalyptus streams) were selected in each of seven regions: Spain, Portugal, Kenya, Central Brazil, South Brazil, Uruguay and Chile (Table 1). Eucalyptus and native streams were selected to represent low-order streams within each forest type in each region and were paired based on size, substrate and geomorphology (three stream pairs per region). Climate, soil, type of native forest and eucalyptus species in plantations varied across regions (Table 1). Differences in water temperature, electrical conductivity, pH and dissolved nutrients across regions reflected differences in climate, geology and vegetation (Table 2). Within each region, streams had similar geomorphology and bedrock; native streams were surrounded by similar vegetation. Streams were small (first–third order; generally < 5 m wide and < 50 cm deep),

Table 1. Location, Climate, Soil and Forest in Seven Regions

Country	Latitude (°)	Longitude (°)	Climate ¹	Soil ²	Native forest	Eucalyptus species
Spain	43.21 to 43.35	− 3.27 to − 3.23	Cfb: warm temperate, fully humid with warm summers	Umbrisols (UM)	Deciduous broadleaf	<i>Eucalyptus globulus</i>
Portugal	40.07 to 40.52	− 8.31 to − 8.20	Csb: warm temperate, warm and dry summers	Umbrisols (UM)	Deciduous broadleaf	<i>Eucalyptus globulus</i>
Kenya	0.41 to 0.47	37.34 to 37.42	As: equatorial, dry summers	Luvisols, Cambisols (LV)	Tropical afro-montane	<i>Eucalyptus globulus</i> or <i>Eucalyptus grandis</i>
Central Brazil	− 15.79 to − 15.73	− 48.07 to − 47.94	Aw: equatorial, dry winters	Ferralsols, Acrisols, Nitisols (FR)	Brazilian savannah	Mixture of <i>Eucalyptus grandis</i> , <i>Eucalyptus saligna</i> , <i>Eucalyptus alba</i> , <i>Eucalyptus urophylla</i> , <i>Corymbia citriodora</i> (previously <i>Eucalyptus citriodora</i>)
South Brazil	− 27.72 to − 27.45	− 52.33 to − 52.06	Cfa: warm temperate, fully humid with hot summers	Ferralsols, Acrisols, Nitisols (FR)	Araucaria rainforest	<i>Eucalyptus grandis</i>
Uruguay	− 34.65 to − 34.18	− 55.31 to − 54.99	Cfa: warm temperate, fully humid with hot summers	Phaeozems (PH) and Kastanozems, Solonetz (KS)	Subtropical seasonal semi-deciduous	Mixture of <i>Eucalyptus globulus</i> and <i>Eucalyptus viminalis</i>
Chile	− 37.69 to − 37.51	− 73.36 to − 73.24	Cfb: warm temperate, fully humid with warm summers	Cambisols (CM)	Coastal deciduous	<i>Eucalyptus globulus</i>

Location of streams, climate, soil, type of native forest and eucalyptus species used in plantations in seven regions.

¹World maps of Köppen–Geiger climate classification: <http://koeppen-geiger.vu-wien.ac.at> (accessed on October 2017); ²World soil resources map: ftp://ftp.fao.org/agl/agll/fao_mwswr/wsavcl.jpg (accessed on October 2017).

with no sign of human impact (except for eucalyptus plantations in eucalyptus streams) (Figure 1).

Leaf Litter Decomposition

Alder (*Alnus glutinosa* (L.) Gaertn.) leaves were collected from the forest floor just after abscission in autumn 2014, in Coimbra, central Portugal. Leaves were air-dried at room temperature in the dark, stored in paper boxes and posted to all teams. *A. glutinosa* is a broadleaf deciduous tree species typical of riparian forests in Europe (Graça and Poquet 2014), but it has been used in decomposition experiments worldwide for comparative pur-

poses (for example, Boyero and others 2011a, b; Ferreira and others 2012; Woodward and others 2012) because it is a highly palatable leaf species to shredders (Graça and others 2001; Azevedo-Pereira and others 2006; Graça and Cressa 2010). Batches of 2.30–2.80 g of air-dry leaves were weighed, sprayed with distilled water to render them soft and avoid breakage during handling and enclosed in fine mesh (FM; 0.5-mm mesh) and coarse mesh (CM; 10-mm mesh) bags (~ 12 × 15 cm). Two mesh sizes were used to allow assessing microbial-driven litter decomposition (FM bags) and litter decomposition driven by both microbes and macroinvertebrates (CM bags). Twelve litter bags of

Table 2. Mean Water Characteristics for Streams in Seven Regions

Regions	Stream type	Channel width (m)	Water depth (m)	Discharge (L s ⁻¹)	Temperature (°C)	Conductivity (µS cm ⁻¹)	pH	Dissolved oxygen (%)	DIN (µg L ⁻¹)	SRP (µg L ⁻¹)
Spain	Native	0.9–1.6	0.1–0.1	34.0–44.0	9.9–11.5	83–101	7.3–7.6	96–98	337–661	4–6
	Eucalyptus	0.6–1.6	0.1–0.2	11.8–54.5	10.7–11.9	73–167	7.1–7.8	94–99	145–307	5–7
Portugal	Native	1.4–2.1	0.1–0.2	16.6–137.0	8.0–8.4	27–36	na	na	69–355	4–6
	Eucalyptus	0.7–1.7	0.1–0.1	22.9–49.2	8.1–10.1	34–44	na	na	161–401	3–5
Kenya	Native	2.4–11.9	0.1–0.3	20.9–944.6	16.5–19.0	33–41	7.7–8	96–102	34–45	18–30
	Eucalyptus	1.3–3.6	0.1–0.4	149.7–367.6	16.6–18.8	34–43	7.5–7.9	90–100	39–51	5–7
Central Brazil	Native	1.1–1.5	0.2–0.3	83.4–219.7	18.9–20.0	4–5	5.2–5.8	65–87	bdl	bdl
	Eucalyptus	0.6–2.0	0.2–0.7	26.7–254.1	16.2–21.6	4–5	4.8–5.4	57–69	bdl	bdl
South Brazil	Native	1.9–2.4	0.1–0.2	36.7–63.0	19.2–20.1	67–76	6.2–6.5	91–101	2–3	84–98
	Eucalyptus	1.1–2.2	0.1–0.5	28.4–151.3	19.4–21.3	59–92	6.1–6.6	86–97	6–22	80–173
Uruguay	Native	2.4–5.2	0.3–0.3	0.5–8.6	22.2–28.4	297–558	8.4–8.7	112–143	170–219	5–8
	Eucalyptus	2.4–4.5	0.3–0.5	1.8–5.1	15.7–24.9	119–276	7.7–8.1	67–128	104–225	2–3
Chile	Native	4.9–10.8	0.2–0.3	295.7–936.4	13.0–19.9	22–37	6.1–6.4	89–98	26–143	5–28
	Eucalyptus	2.3–11.9	0.1–0.2	24.2–1060.0	12.8–13.9	32–39	6.4–6.5	84–89	10–51	23–88

Mean water characteristics (min–max) for streams ($n = 3$) flowing through native forests and eucalyptus plantations in seven regions. Water temperature was assessed with dataloggers or field probes, electrical conductivity, pH and dissolved oxygen were assessed with field probes, and dissolved nutrients were assessed by ion chromatography (generally, $n = 2$ –4; water temperature in Spain, $n = 31$; channel width, depth and discharge in Kenya, $n = 12$). DIN dissolved inorganic nitrogen, SRP soluble reactive phosphorus, na not assessed, bdl below detection limit (100 µg L⁻¹).

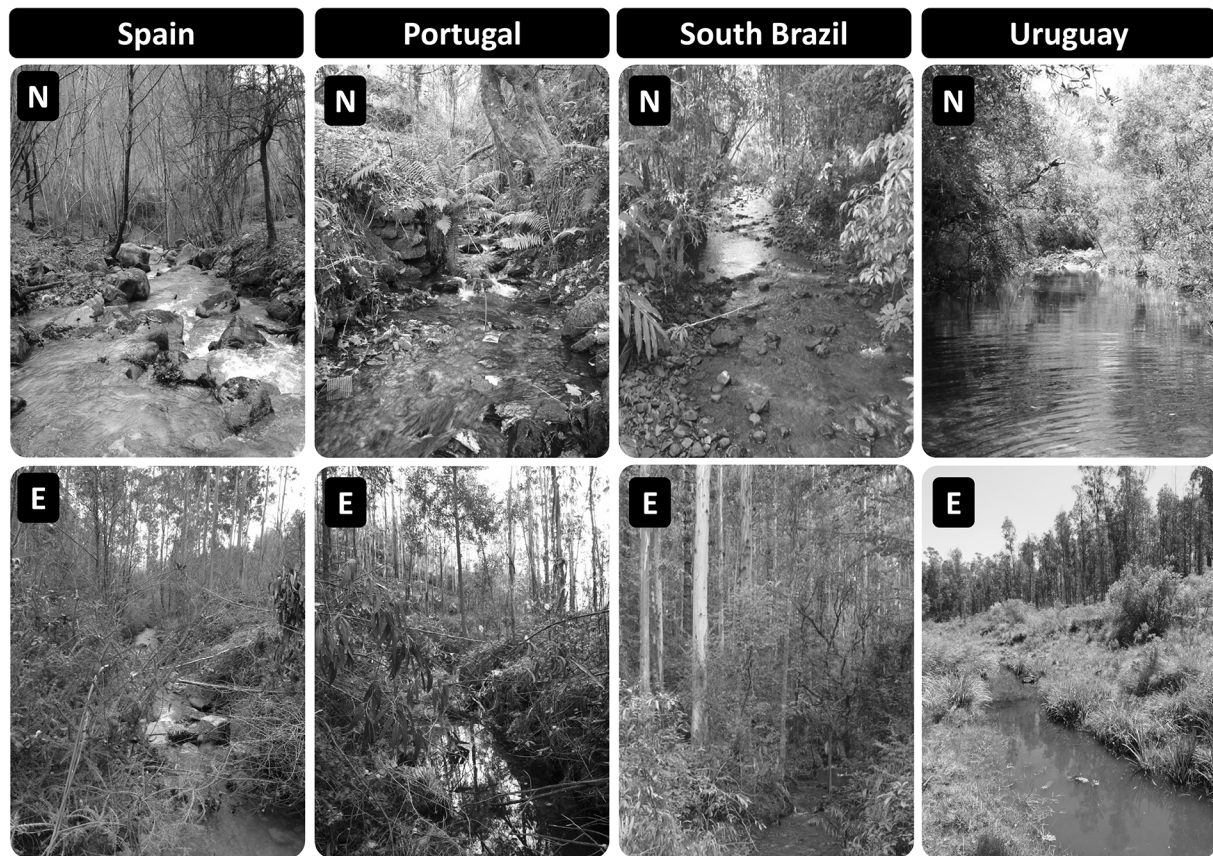


Figure 1. Examples of streams flowing through native forests (N) and eucalyptus plantations (E).

each mesh size were deployed along a 50-m reach in each stream.

Additionally, sets of six litter bags from each mesh size were prepared as described above, taken to the field on day 0 and submerged for about 10 min in one stream per region. Litter bags were taken back to the laboratory, and litter was oven-dried (60°C , ≥ 48 h) and weighed for the determination of initial oven-dry mass that allowed computing an initial air-dry mass to initial oven-dry mass conversion factor taking into account handling losses. This conversion factor was used to estimate the initial oven-dry mass of the samples.

Replicate litter bags ($n = 4$) were sampled on three occasions over the incubation period that lasted for 21–60 days, between November 2014 and February 2016. Maximum incubation period and sampling dates varied across regions, but not across streams within regions, and were defined to allow at least 50% mass loss in coarse mesh bags. Litter bags were retrieved, enclosed individually in plastic bags and taken to the laboratory in an ice chest. Leaves were rinsed with running tap water over a 0.5-mm mesh sieve to retain small leaf fragments, oven-dried (60°C ,

≥ 48 h) and weighed for the determination of remaining dry mass (DM). Decomposition rates (k ,/d) were estimated by fitting a negative exponential model to the fraction of mass remaining over time; $\text{DMt}/\text{DMi} = e^{-kt}$, where DMt is the DM remaining at time t (d), DMi is the initial DM and k is the decomposition rate on a daily basis. Since streams differed in water temperature, decomposition rates were also estimated on a degree-day basis (k ,/dd) by replacing time in the model above by the cumulative thermal sum at the sampling date, and these values were used for the analyses.

Data Analysis

The overall effect of eucalyptus plantations on stream water and alder leaf litter decomposition, and the effects of region and mesh size on the magnitude and direction of the response of these variables to plantations were assessed using meta-analytic techniques. These are most often used in the context of systematic reviews, but can also be applied to multisite studies (Rustad and others 2001; Walker and others 2006; Gurevich 2013).

The response of water characteristics and alder leaf litter decomposition to the replacement of native forests by eucalyptus plantations (effect size) was estimated as the response ratio (R), which is given by the ratio of the variable of interest (for example, litter decomposition rate) in the eucalyptus stream (k_E) to the variable of interest in the paired native stream (k_N) ($R = k_E/k_N$); $R = 1$ indicates no effect of eucalyptus plantations, $R < 1$ indicates an increase and $R > 1$ indicates a decrease in the variable of interest in eucalyptus streams (Hedges and others 1999). Values were $\ln$ -transformed ($\ln R$) for the analyses. The variance associated with the effect size ($V_{\ln R}$), which is needed to weigh each effect size by its precision, was estimated from the standard deviation and sample size associated with each mean value.

The overall response of the variable of interest to eucalyptus plantations was determined using a random-effects model of meta-analysis; between-study variance was estimated by the restricted maximum likelihood method (Borenstein and others 2009). The effects of mesh size (that is, type of decomposer community) and region on the magnitude and direction of the response of the variable of interest to eucalyptus plantations were assessed by subgroup analyses. For the interpretation of the results, R values were converted into percentage of change with 0% indicating no effect of eucalyptus plantations, negative values indicating percentage decrease and positive values indicating percentage increase of the variable of interest in eucalyptus streams. A significant effect existed if the 95% CL did not include 0, and effects were significantly different if their 95% CLs did not overlap (Q_M , $p < 0.050$; Borenstein and others 2009). The percentage of total variability that was due to between-study variation rather than sampling error (I^2) was also calculated (Borenstein and others 2009). Analyses were performed with OpenMEE software (Wallace and others 2017).

RESULTS

Stream Characteristics

Overall channel width was significantly lower in eucalyptus than in native streams, although differences between stream types were consistently non-significant within each region (Table 2 and Table S1). Overall water depth and dissolved inorganic nitrogen (DIN) did not significantly differ between stream types, although eucalyptus streams were significantly deeper than native streams in Uruguay (by 40%) and shallower in Portugal (by

26%) and DIN concentration was significantly lower in eucalyptus than in native streams in Spain (by 58%). Discharge and oxygen saturation did not significantly differ between eucalyptus and native streams at the regional or overall level.

Overall water temperature, conductivity, pH and soluble reactive phosphorus (SRP) did not significantly differ between eucalyptus and native streams, but there were significant differences between stream types in some regions. Temperature was significantly higher in eucalyptus than in native streams in Portugal (by 18%) and lower in Uruguay (by 21%); conductivity was significantly lower in eucalyptus streams in Chile (by 8%) and in Uruguay (by 54%); pH was significantly higher in eucalyptus streams in South Brazil (by 4%) and lower in Uruguay (by 7%); and SRP concentration was significantly lower in eucalyptus streams in Kenya (by 74%) and in Uruguay (by 73%) (Table 2 and Table S1).

Leaf Litter Decomposition

Alder leaf litter decomposition rates varied 15-fold in FM bags across regions, from 0.00024/dd in native streams in Central Brazil to 0.0037/dd in native streams in Kenya, and sixfold in CM bags, from 0.0009/dd in native streams in Central Brazil to 0.0049/dd in native streams in Portugal, being generally higher in CM than in FM bags (k_{CM}/k_{FM} , range: 1.0–3.9, mean: 2.2) (Figure 2).

The overall response of litter decomposition rates to eucalyptus plantations was an apparent decrease by 11%, which was non-significant (95% CL: – 24 to 5%) (Figure 3), but the percentage of total variation explained by between-study variation was high ($I^2 = 93\%$), suggesting that differences in mesh size and region may moderate the response of litter decomposition to forest change. When responses were considered per mesh size, no significant effect was found for FM bags (95% CL: – 16 to 29%), whereas an overall significant decrease by 23% (95% CL: – 39 to – 3%) was found for CM bags (Figure 3), although the difference between mesh sizes was non-significant ($Q_M = 3.586$, $df = 1$, $p = 0.058$). The percentage of total variation explained by between-study variation was, however, high for both FM and CM bags ($I^2 = 93\%$ and 92% , respectively).

The response of litter decomposition to plantations significantly differed across regions for FM bags ($Q_M = 25.238$, $df = 6$, $p < 0.001$), with a significant increase in litter decomposition in eucalyptus streams by 110% (95% CL: 11–300%) for Central Brazil and by 32% (95% CL: 13–54%) for

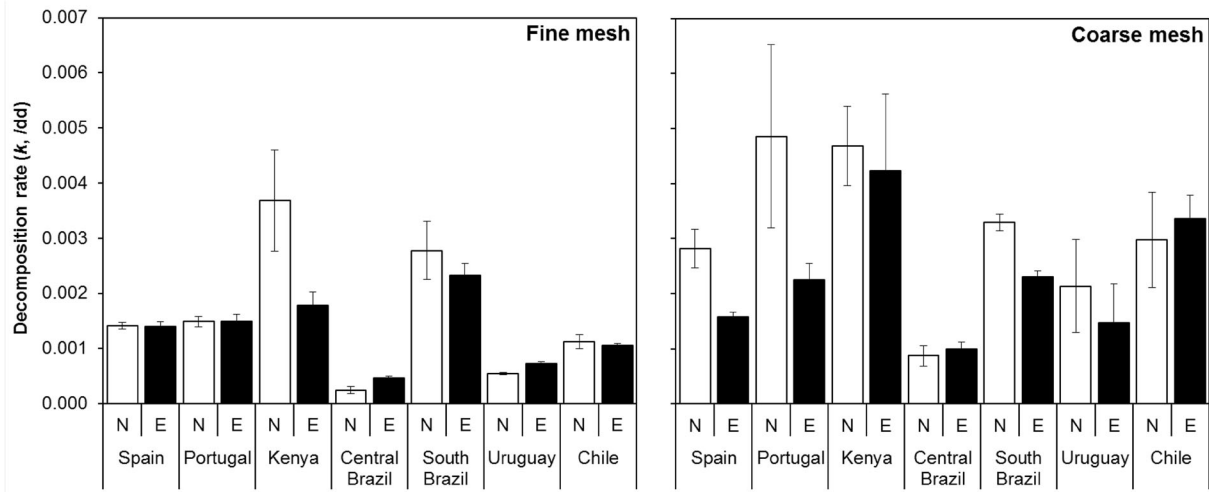


Figure 2. Litter decomposition rates (mean $\pm$ standard error, $n = 3$) in fine mesh and coarse mesh bags incubated in native (N) and eucalyptus (E) streams in seven regions.

Uruguay and nonsignificant effects for the remaining regions (for Kenya the effect was marginally non-significant: mean decrease by 48%; 95% CL: -73 to 0.2%) (Figure 3).

For CM bags, the response of litter decomposition to plantations did not significantly differ across regions ($Q_M = 7.498$, $df = 6$, $p = 0.277$), although a significant decrease was found for Spain (-41% ; 95% CL: -52 to -27%), South Brazil (-31% ; 95% CL: -41 to -19%) and Uruguay (-36% ; 95% CL: -49 to -20%), while no significant effects were found for the remaining regions (for Portugal the effect was marginally non-significant: mean inhibition by 50% ; 95% CL: -75 to 3%) (Figure 3). There was a high variation in some regions (for example, Central Brazil for FM bags and Kenya, Central Brazil and Chile for CM bags; Figure 3) suggesting that local (stream) conditions moderate the response of litter decomposition to forest change.

DISCUSSION

Our first global assessment of the effects of eucalyptus plantations on stream ecosystem functioning shows that such effects depend on the type of decomposer communities (microbes only or microbes + macroinvertebrates) and vary among different regions across the distribution area of eucalyptus plantations. The observed variation in the response of litter decomposition to eucalyptus plantations suggests that we cannot make generalizations across regions. In regions where shredders are abundant (as indicated in previous studies), eucalyptus plantations seem to inhibit

litter decomposition by affecting shredder communities. Microbial-driven litter decomposition may also respond to eucalyptus plantations, especially if these are accompanied by changes in dissolved nutrient availability, litter characteristics or solar irradiation. The present study builds up on the meta-analysis by Ferreira and others (2016) by showing that, indeed, results from studies in the Iberian Peninsula cannot be extrapolated to other regions since there are regions where total litter decomposition was not overall affected by eucalyptus plantations and there are regions where microbial-driven litter decomposition was affected by plantations, contrarily to what has been observed for the Iberian Peninsula.

There was an overall reduction of total litter decomposition (that is, in CM bags) in streams flowing through eucalyptus plantations, whereas there were no overall effects on microbial-driven litter decomposition (that is, in FM bags). This agrees with results from the largest previous study comparing leaf litter decomposition between native and eucalyptus streams in the Iberian Peninsula (5 stream pairs in each of Portugal and Spain; Ferreira and others 2015), which reported a mean decrease by 42% for litter decomposition in CM bags in eucalyptus streams, while litter decomposition in FM bags was less affected (mean decrease by 7%). Also, a meta-analysis of 10 primary studies assessing the effects of eucalyptus plantations on leaf litter decomposition in Iberian streams showed a stronger decrease of litter decomposition in CM bags (mean decrease by 36%) than in FM bags (mean decrease by 7%) (Ferreira and others 2016). Thus, our present results are consistent with those

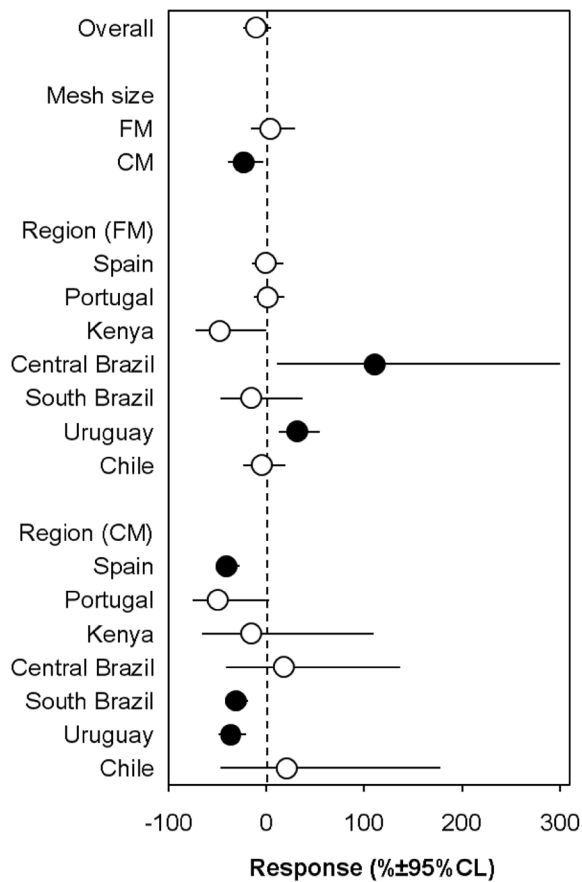


Figure 3. Response of litter decomposition to eucalyptus plantations (% change), overall, per mesh size and per region. The dashed line (0%) indicates no effect of eucalyptus plantations, positive values indicate percentage increase, and negative values indicate percentage decrease of litter decomposition in eucalyptus streams. Significant effects exist when the 95% CL does not include 0 (black symbols), and effects significantly differ between levels within each moderator if their 95% CLs do not overlap. *CM* coarse mesh, *FM* fine mesh.

reported previously for the Iberian Peninsula, which suggested that the effects of eucalyptus plantations on litter decomposition are mediated through effects on shredders.

In fact, taxon richness, density or biomass of benthic macroinvertebrates (including shredders) are generally lower in streams in *E. globulus* plantations than in streams in native deciduous forests in the Iberian Peninsula (Abelho and Graça 1996; Larrañaga and others 2009a, b; Ferreira and others 2015; Cordero-Rivera and others 2017; some of these streams were used in the present study). Also, changes in shredders trait distribution have been reported when native deciduous forests are replaced by *E. globulus* plantations, including a de-

crease in species with long life cycles, large body sizes and feeding on coarse particulate organic matter in eucalyptus streams (Larrañaga and others 2009a). These changes can be partially explained by increased intermittency in eucalyptus streams. It has been shown that the density of benthic macroinvertebrates (and of shredders in particular) decreases with decreasing flow permanence and increasing duration and frequency of drying events, leading to a reduction of litter decomposition rates (Datry and others 2011).

Changes on benthic macroinvertebrate communities in eucalyptus streams may also be due to changes in the characteristics of litter inputs (Larrañaga and others 2014). For instance, streams flowing through mixed native deciduous forests in the Iberian Peninsula receive most of the litter fall in autumn and winter; this diverse litter input is composed of litter species with distinct characteristics, ranging from soft, nutrient-rich to tough, nutrient-poor litter (Abelho and Graça 1996; Pozo and others 1997; Molinero and Pozo 2004; some of these streams were used in the present study). On the contrary, streams flowing through *E. globulus* plantations receive litter throughout the year, with a peak in summer (Abelho and Graça 1996; Pozo and others 1997; Molinero and Pozo 2004). This accumulation of eucalyptus litter in the benthos at a time of low flow may contribute to the formation of pools with detrimental conditions for aquatic life, that is, high concentration of toxic leaf leachates (Canhoto and Laranjeira 2007; Canhoto and others 2013; Gama and others 2014). Also, eucalyptus leaves have high concentration of secondary compounds with antimicrobial activity (for example, polyphenols and essential oils) and a thick waxy cuticle (Molinero and others 1996; Pozo and others 1997; Canhoto and Graça 1999; Molinero and Pozo 2006; Hepp and others 2009), which makes them a poor resource for shredders (Canhoto and Graça 1995, 1999). The sub-optimal eucalyptus resource, when compared with some native litter species, may lead to reduced growth and survival of shredders (Canhoto and Graça 1995; Correa-Aranda and others 2015; Kiffer and others 2018), which in the long term may result in depleted macroinvertebrate communities.

Additionally, changes in benthic macroinvertebrate communities may be driven by modifications in fish communities induced by forest change. Increases in solar exposition (for example, by replacing wide canopy species by single-stemmed eucalyptus trees) can lead to increases in fish densities (Teixeira-de-Mello and others 2015) that may prey on macroinvertebrates and reduce their

densities in eucalyptus streams (Mcintosh and others 2005). Given that fish species richness and densities are generally higher in subtropical than in temperate regions (Teixeira-de-Mello and others 2012), effects of forest change on fish communities might be stronger in streams in the former regions.

Although the effect of eucalyptus plantations on total litter decomposition did not significantly differ across regions, it was significant or nearly significant only for regions with temperate climate (Spain, Portugal, South Brazil and Uruguay). This suggests that changes in macroinvertebrate communities induced by eucalyptus plantations reported for temperate climates cannot be extrapolated to other climatic zones. The highly variable effect of eucalyptus plantations on total litter decomposition in Kenya, Central Brazil and Chile (for example, varying from strong decrease, to no effect, to strong increase within a single region), which resulted in nonsignificant effects of eucalyptus plantations at the regional level, may be due to variation in local factors as discussed below.

Shredder abundance is low in some Kenyan streams (Dobson and others 2002), and thus, litter decomposition could be primarily mediated by microbes in these streams (Dobson and others 2004), while shredders contribute substantially to litter decomposition in other streams (Boyero and others 2015). A negligible contribution of shredders to litter decomposition has been found also in some tropical streams in Central and South America, including the Brazilian savannah (Gonçalves and others 2006, 2007; Camacho and others 2009; Boyero and others 2015), whereas shredder abundance and richness seem to increase with elevation in different tropical regions (Camacho and others 2009; Yule and others 2009). This variation in shredder abundance in tropical streams may explain why litter decomposition is inhibited by eucalyptus plantations in some streams whereas no effect is observed in others. Additionally, the higher litter decomposition in one of the eucalyptus streams in Kenya may be attributed to the much higher discharge in this stream when compared with the native stream (368 vs. 21 L/s). Also, the higher litter decomposition in eucalyptus streams in Central Brazil could be due to eucalyptus leaves being of higher nutritional quality than native leaves (Gomes and others 2018), which may result in higher microbial inoculum potential in eucalyptus streams. Eucalyptus plantations in Central Brazil were also more diverse than in other regions (Table 1), which may have ensured a higher diversity of substrates for aquatic communities in eucalyptus streams in this region when compared

with eucalyptus streams in other regions. The strong stimulation of litter decomposition in some eucalyptus streams in Chile could result from less recalcitrant litter in these streams than in native streams where some of the endemic tree species contribute with litter that is tough and has high lignin and secondary compounds concentrations (Muñoz-Concha and others 2004). This variation in the effects of eucalyptus plantations on leaf litter decomposition reinforces the suggestion that effects are stronger for streams where shredders are well represented, but may depend on local factors (Pozo and others 1998; see above).

Litter decomposition in fine mesh bags was not overall affected by eucalyptus plantations, but there were significant differences across regions. Microbial decomposers generally differ between streams in *E. globulus* plantations and streams in native deciduous forests in the Iberian Peninsula (Chauvet and others 1997; Bärlocher and Graça 2002; Ferreira and others 2006; some of these streams were used in the present study), but this is not generally translated into altered microbial-driven litter decomposition (Ferreira and others 2016; this study), suggesting high functional redundancy in microbial communities in those areas. Contrarily to what has been observed in the Iberian Peninsula, microbial-driven litter decomposition was significantly stimulated in eucalyptus streams in Central Brazil and Uruguay and nearly significantly inhibited in Kenya, which suggests that functional redundancy in microbial decomposer communities is not universal. In Kenya, microbial-driven litter decomposition was lower in eucalyptus streams that had significantly lower soluble reactive phosphorus concentrations than native streams, which may have hindered microbial activity and litter decomposition in the former streams (Gulis and others 2006). In Central Brazil, microbial-driven litter decomposition was higher in eucalyptus than in native streams likely due to the better quality of eucalyptus than native leaves as mentioned above (Gomes and others 2018). In Uruguay, microbial-driven litter decomposition was also higher in some eucalyptus than in native streams, which may be partially explained by the fact that some eucalyptus streams were exposed to solar irradiation since plantations were not present in the stream banks (Figure 1). Exposure to solar irradiation, by allowing the development of primary producers, may have facilitated a priming effect by which microbial decomposers would benefit from labile carbon produced by algae and decompose more recalcitrant substrates (that is, litter) at faster rates (Danger and others 2013; Kuehn and others 2014).

Our results show that, even if eucalyptus streams are surrounded by trees, providing shade and organic matter, they endure multiple changes that result in altered ecosystem functioning, which may jeopardize their ability to provide ecosystem services. The ratio of litter decomposition rates at impacted and reference sites ($k_{\text{imp}}/k_{\text{ref}}$), which is equivalent to the response ratio used here ($R = k_E/k_N$), was proposed as a metric to assess functional stream integrity (Gessner and Chauvet 2002). We found that total litter decomposition (in CM bags) should be addressed for an accurate evaluation of eucalyptus effects on ecosystem functioning, whereas microbial-driven litter decomposition (in FM bags) is preferable when shredders are rare or absent and physical abrasion by current and sediments is a possibility. The use of litter decomposition as a bioassessment tool has several advantages compared with several methods based on structural characteristics of stream ecosystems (Bonada and others 2006). First, it is a fundamental ecosystem process, and thus, it allows assessing stream functional integrity, which is intimately linked with the ability of the system to provide services. Secondly, it is not based on taxonomic identification, and thus, it allows cross-regional comparisons of forest change effects on streams. In addition, it is easy to standardize and implement, even in comparison with other stream processes (von Schiller and others 2017). Thus, the response ratio is a useful approach to address forest change effects on stream ecosystem functioning (Ferreira and others 2015, 2016). This is especially relevant at a time of intense forest change with the increase in the area occupied by commercial tree plantations, changes in forest composition due to climate change (for example, increase in drought-tolerant and decrease in drought-sensitive species in a scenario of increasing aridity) and invasion of native forests by exotic species (Kominoski and others 2013).

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Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest.

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