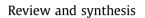
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A meta-analysis on the effects of changes in the composition of native forests on litter decomposition in streams





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ABSTRACT

Native forest replacement by plantations and invasions by exotic plant species are occurring worldwide. We conducted a meta-analysis of studies reporting the effects of these forest changes on litter decomposition in streams. Overall, forest change significantly inhibited litter decomposition rate by ca 18%. However, only the replacement of native forests by deciduous broadleaf or eucalyptus (Eucalyptus globulus) plantations resulted in significant inhibition of litter decomposition (26% and 22%, respectively) whereas conifer plantations or the invasion by exotic species did not significantly affect litter decomposition. The replacement of native forests by eucalyptus plantations was the most common type of forest change in our database. The effect of eucalyptus plantations on litter decomposition was significant when they were present simultaneously at the catchment and riparian scales and when native litter input was replaced by eucalyptus litter input in a manipulative experiment at the stream reach level. This suggests that a strong effect of eucalyptus plantations on ecosystem functioning is mediated by changes on litter inputs to streams. Eucalyptus plantations significantly inhibited the decomposition of high quality litter and total leaf litter decomposition but not the decomposition of wood and low quality leaves, or microbial-driven leaf litter decomposition. This indicates that eucalyptus plantations inhibit (likely through changes in litter inputs) litter decomposition by affecting detritivores. Eucalyptus plantations may thus have stronger negative effects on decomposition rates in streams receiving high quality litter and where detritivores are abundant. The presence of native tree species in the riparian area may mitigate the negative effects of eucalyptus plantations on stream processes. The inhibitory effect of deciduous broadleaf plantations on litter decomposition was likely due to beech (Fagus sylvatica) being used in the majority of the plantations, and beech litter is of low quality for detritivores and decomposers. The lack of significant effects of conifer plantations and invasions might be due to contrasting effects of the different conifer or invasive species on decomposers. This meta-analysis also identified several research gaps that may guide future studies on the effect of forest change on stream functioning.

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Contents

| 1. | Introd | ction | 28 | | | | |
|--------------------------|--------|---|----|--|--|--|--|
| 2. Materials and methods | | | | | | | |
| | | Literature search and selection of relevant primary studies | | | | | |
| | | Effect size | | | | | |
| | 2.3. | Noderator variables | 29 | | | | |
| | 2.4. | Data analyses | | | | | |
| | | 2.4.1. Overall effect size | 30 | | | | |
| | | 2.4.2. Moderator analyses | 30 | | | | |
| | | 2.4.3. Publication bias | 30 | | | | |
| | | 2.4.4. Sensitivity analysis | 31 | | | | |

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| 3. | Result | ts | . 31 |
|----|--------|---|------|
| | 3.1. | Overview of studies | |
| | 3.2. | Overall effect of forest change on litter decomposition in streams | . 31 |
| | 3.3. | Effects of type of forest change on litter decomposition in streams | . 31 |
| | 3.4. | Replacement of native broadleaf forests by eucalyptus plantations | . 31 |
| | 3.5. | Replacement of native deciduous broadleaf forests by deciduous broadleaf plantations | . 32 |
| | 3.6. | Replacement of native deciduous broadleaf forests by conifer plantations | . 32 |
| | 3.7. | Invasions of native forests by exotic woody species | . 33 |
| | 3.8. | Sensitivity analyses | . 33 |
| 4. | Discu | ssion | . 33 |
| | 4.1. | Overall effect of forest change on litter decomposition in streams | . 33 |
| | 4.2. | Replacement of native broadleaf forests by eucalyptus plantations | |
| | 4.3. | Replacement of native deciduous broadleaf forests by deciduous broadleaf plantations | . 34 |
| | 4.4. | Replacement of native deciduous broadleaf forests by conifer plantations | . 35 |
| | 4.5. | Invasions of native forests by exotic woody species | . 35 |
| | 4.6. | Forecasting litter decomposition responses based on plant trait similarity between native and altered forests | . 35 |
| | 4.7. | Comparison of streams flowing through native versus altered forests and comparison of native versus exotic litter | . 36 |
| 5. | Concl | usion | . 36 |
| | Ackno | owledgements | . 36 |
| | Appe | ndix A. Supplementary material | . 36 |
| | Refer | ences | . 36 |
| | | | |

1. Introduction

In small forest streams, autochthonous primary production is limited by low solar irradiation and the decomposition of litter produced by the terrestrial vegetation is a fundamental ecosystem process that fuels aquatic food webs with carbon (C), nutrients and energy (Vannote et al., 1980; Wallace et al., 1997). The decomposition of organic matter is carried out mainly by microbes (mostly aquatic hyphomycetes) and invertebrate detritivores (Hieber and Gessner, 2002; Pascoal and Cássio, 2004) and is highly sensitive to changes in environmental conditions (Gessner and Chauvet, 2002; Young et al., 2008). Given the heterotrophic nature and high aquatic-terrestrial interface of these small streams, aquatic communities and processes are highly vulnerable to changes in the surrounding vegetation.

Forest clearance (e.g. conversion into pasture or agriculture) has strong effects on aquatic communities and ecosystem functioning as the system shifts from heterotrophic to autotrophic in response to the decrease in litter inputs and increase in solar irradiation (Hladyz et al., 2011a). The replacement of native forests by commercial tree plantations, or their invasion by exotic woody species, can also affect aquatic communities and processes despite the fact that the heterotrophic nature of the streams is generally maintained, i.e. shade continues to be provided and foodwebs are based on the decomposition of allochthonous litter (Graça et al., 2002: Kominoski et al., 2013). However, the studies addressing the effects of the replacement of native forests by tree plantations or their invasion by exotic woody species on litter decomposition often show contrasting results. For instance, previous studies reported stimulation (Whiles and Wallace, 1997; Lecerf et al., 2007; Menéndez et al., 2013), inhibition (Abelho and Graca, 1996; Kennedy and Hobbie, 2004; Lecerf and Chauvet, 2008), or no major difference (Bärlocher and Graça, 2002; Lecerf et al., 2005; Riipinen et al., 2010; Hisabae et al., 2011) in litter decomposition rates in streams flowing through altered forests when compared with streams flowing through native forests.

The variability in the reported results suggests that the effects of forest change could be moderated by other factors. For instance, the replacement of native forests by tree plantations with very dissimilar traits (e.g. deciduous vs. evergreen species) is likely to produce stronger effects on streams than the replacement by trees with similar traits (e.g. mixed deciduous broadleaf forest vs. deciduous broadleaf tree plantations) or moderate invasion by exotic species (Kominoski et al., 2013). In addition, stronger effects might be expected when forest changes occur both at the catchment and riparian level than only in the riparian area or at the catchment level. The effects may also differ depending on whether they are driven by changes in litter inputs (stronger when forest change occurs at the riparian level) or by changes in hydrology and water chemistry (stronger when forest change occurs at the catchment level).

The effects of forest change may also depend on physical and chemical litter properties; the decomposition of soft, high nutrient (low C:nutrient ratio) litter is likely to respond to forest change if this affects detritivores, while the decomposition of tough, low nutrient litter is likely to be less sensitive to forest change since this is mostly carried out by microbial decomposers, whose communities are reported to be functionally redundant (Dang et al., 2005; Ferreira et al., 2006; Gulis et al., 2006). High quality litter may also decompose faster in streams flowing through tree plantations if it acts as an island of good quality resource in a streambed of recalcitrant litter (e.g. *Alnus glutinosa* litter in streams flowing through eucalyptus or conifer plantations); when given a choice, detritivores prefer soft, high quality litter (Canhoto and Graça, 1995).

Total litter decomposition (i.e. carried out by both microbes and invertebrates) is likely to be more sensitive to forest change than microbial-driven litter decomposition if invertebrates are the main players on litter decomposition (Gulis et al., 2006). Also, since invertebrate activity on decomposing litter highly depends on microbial conditioning (Canhoto and Graça, 2008), any negative effects of forest change on microbes may be amplified by invertebrates.

The region where forest change takes place can also moderate the magnitude of its effect on litter decomposition. Streams in drier regions such as in the Mediterranean may dry out during the warmer months and it has been shown that these streams have lower invertebrate richness than permanent streams (Datry et al., 2011). Intermittent streams may thus be more susceptible to further environmental changes as forest change than streams in humid regions (Ferreira et al., 2006).

Changes in dissolved nutrient availability could also moderate the effect of forest change on litter decomposition (Molinero et al., 1996; Diez et al., 2002). If the replacement of native forests by plantations with poorer litter quality is accompanied by an increase in dissolved nutrient availability due to fertilization or atmospheric nitrogen deposition, microbial conditioning of submerged litter might be stimulated and differences in litter decomposition rates between native and altered streams might be limited.

Here we present a systematic review of 24 studies addressing the effect of forest change on litter decomposition in streams and published between 1993 and 2015. Using meta-analysis, we (i) determine the magnitude and direction of the mean effect of forest change on litter decomposition, (ii) assess which characteristics of the incubation conditions influence the magnitude of the effects and (iii) identify research gaps that could guide future studies on the effect of forest change on stream functioning.

2. Materials and methods

2.1. Literature search and selection of relevant primary studies

We searched for primary studies that addressed the effect of forest change on litter decomposition in streams published between January 1970 and September 2015 in English, French, Portuguese and Spanish. The search was done using Google Scholar, personal literature databases and reference lists in primary studies and in review papers. The following combinations of search terms and their equivalents in French, Portuguese and Spanish were used in Google Scholar: decomposition or processing or breakdown or decay, combined with litter or leaf or leaves or bark or wood, with eucalyptus or conifer or invasive or exotic or 'exotic species names', and with stream or river.

Primary studies were included in the analysis if they satisfied the following criteria: (i) they aimed at addressing the effect of forest change on litter decomposition in streams, (ii) they compared at least one stream flowing through a native forest (native stream, NAT) and one stream flowing through an altered forest (altered stream, ALT) such as deciduous broadleaf plantation, conifer plantation or eucalyptus plantation or a forest invaded by exotic woody species, (iii) they reported decomposition of natural litter (i.e. leaves, bark or wood such as sticks, twigs or veneers) rather than artificial substrates such as cotton strips or cellulose, (iv) they used litter of allochthonous origin (i.e. riparian trees or grass) rather than macrophytes, and (v) they reported sample size and a measure of variation (the latter not necessarily mandatory) for both NAT and ALT streams. Criteria (i) and (ii), although potentially restricting the number of studies considered in this review, give some assurance that the NAT and ALT streams are comparable in all other characteristics since it was the authors' goal to addressed the effects of forest change on litter decomposition. Criteria (iii) and (iv) allow to focus on the process that is at the base of foodwebs in forest streams, i.e. the decomposition of terrestrial derived organic matter. Twenty-six studies satisfied the above inclusion criteria (Appendix S1). However, due to double publication, two studies were excluded from the analysis (Elosegi et al., 2006; Riipinen et al., 2009) and the final database was composed of 24 studies (Appendix S1).

We considered as a case study each comparison of a NAT stream and an ALT stream. The NAT–ALT pairs were either defined in the primary study or specified after personal communication with the authors. Multiple publications of the same data were common and care was taken to have each case study represented only once in the database (Appendix S1). Many individual studies contributed several unique NAT–ALT comparisons to the database, for instance for different litter species, mesh sizes or regions (e.g. Bärlocher and Graça, 2002; Ferreira et al., 2006, 2015; Hladyz et al., 2011a), making a total of 156 case studies. Although several cases derived from the same study are non-independent, their omission from this review would have restricted our analysis of moderators. We have therefore included multiple cases per study into analysis, but assessed their effect on the results in a sensitivity analysis.

2.2. Effect size

The effect size of forest change on the exponential litter decomposition rate per degree-day (k, dd^{-1}) was calculated as the natural logarithm of the response ratio, i.e. the ratio of litter decomposition in the altered stream (k_{ALT}) to litter decomposition in the native stream (k_{NAT}) , lnR = ln (k_{ALT}/k_{NAT}) .

If litter decomposition was reported as exponential decomposition rate per degree-day, which was most often the case, it was used directly in the calculation of the effect size. If litter decomposition rate was reported per day, percentage litter mass remaining or percentage litter mass lost, it was converted into decomposition rate per degree-day.

The variance associated with each lnR value (V_{lnR}) was calculated from the standard deviation (SD) associated with each decomposition rate value (Koricheva et al., 2013). If variation in the primary studies was reported as standard error (SE) or confidence limit (CL), then it was converted into SD. In some cases, no measure of variance associated with decomposition rates was given in the primary studies and therefore missing SD values were estimated by imputation based on the cases in the database that reported SD values associated with decomposition rates (Lajeunesse, 2013). However, since any estimation of decomposition rates or SD would have a certain degree of inaccuracy, an attempt was made to contact the authors of the primary studies to obtain decomposition results as k in dd⁻¹ and variation as SD to reduce estimations to the minimum. Despite this, estimates of values had to be made for 37% of cases (k in dd^{-1} and SD combined). We have assessed the effect of using estimated data in a sensitivity analysis.

2.3. Moderator variables

Several biotic and abiotic explanatory variables, referred to as moderators in meta-analysis, may affect the magnitude of the response of litter decomposition rate to forest change (Table 1). The moderators considered in this meta-analysis correspond to our hypotheses regarding factors likely to influence the relationship between forest change and litter decomposition. These included type of forest change (replacement of native forests by deciduous, conifer or eucalyptus plantations or invasion of native forests by exotic woody species), extent of forest change (change in vegetation in the catchment but not in the riparian zone, in the catchment and riparian zone, or only in the riparian zone), type of native forest (deciduous broadleaf, evergreen broadleaf or eucalyptus), identity of the dominant species in plantations or of invasive woody species (several), origin (native or exotic), type (leaves, needles, wood or mixture) and identity (several) of the incubated litter, type of the decomposing community (microbial or total, i.e. microbes plus invertebrates), country (several) and ratio between dissolved inorganic nitrogen (DIN) or phosphorus (P) in ALT and NAT streams (continuous variable). Information on moderators was extracted from primary studies when available, otherwise the authors were contacted (Table S1). The description of moderators and levels within moderators is given in Table S2.

2.4. Data analyses

All statistical analyses were performed in RStudio (RStudio, 2012) with the metafor package (Viechtbauer, 2010).

Table 1

Structure of the database (n = 156) showing the number of cases per moderator variable. Description of moderators is given in Table S2.

| Forest change type | Eucalyptus ($n = 92$) | | Conifer (<i>n</i> = 26) | | Deciduous $(n = 21)$ | | Invasion (<i>n</i> = 17) | |
|---|--|----------------|--|-------------|-------------------------------------|----------|-------------------------------------|---|
| Moderator | Level | n | Level | n | Level | п | Level | n |
| Extent of change | Catchment | 11 | Catchment | 6 | Catchment + Riparian | 16 | Catchment + Riparian | |
| | Catchment + Riparian Binggian | 59 | Catchment + Riparian | 20 | Riparian | 1 | Riparian | 1 |
| | Riparian Stream | 18 4 | | | na | 4 21 | | |
| Native forest type | Deciduous broadleaf forest | 74 | Deciduous broadleaf forest | 22 | Deciduous broadleaf forest | 21 | Deciduous broadleaf forest | |
| | Green broadleaf forest | 18 | Green broadleaf forest | 4 | | | Eucalyptus forest | |
| | | | | | | | Deciduous and conifer forest | |
| dentity of species in plantations or of invasive species | Eucalyptus globulus | 92 | Conifer mixture Cryptomeria japonica | 8 4 | Fagus sylvatica Platanus hybrida | 20 1 | Fallopia japonica Rhododendron | |
| | | | Larix sibirica + Betula pubescens | 2 | | | ponticum Salix babylonica | |
| | | | Picea abies + Abies alba Pinus radiata Pinus strobus | 4 6 2 | | | Prunus padus Tamarix ramosissima | |
| itter origin | Native Exotic (<i>Eucalyptus</i>) | 70 22 | Native Exotic | 23 3 | Native | 21 | Native Exotic | |
| itter type | Leaves Mixture Wood | 64 18 10 | Leaves Needles | 19 7 | Leaves | 21 | Leaves | |
| Aquatic community type | Microbial | 22 | Microbial | 6 | Microbial | 10 | Microbial | |
| | Total | 70 | Total na | 18 2 | Total | 11 | Total | |
| itter identity | Alnus Castanea | 29 6 | Acer Alnus | 1 9 | Alnus Quercus | 11 10 | Alnus Eucalyptus | |
| | Eucalyptus | 22 | Betula | 1 | Quercus | 10 | Fallopia | |
| | Mixture | 9 | Cryptomeria | 2 | | | Fraxinus | |
| | Quercus | 24 | Euptelea | 2 | | | Quercus | |
| | Pinus | 2 | Larix | 1 | | | Prunus | |
| | | | Pinus Quercus | 4 6 | | | Rhododendron Salix | |
| | | | Quercus | 0 | | | Tamarix | |
| ountry | Portugal | 28 | Britain | 4 | France | 16 | Australia | |
| | Spain USA | 46 18 | Iceland Ireland | 2 4 | Spain Sweden | 1 4 | England France | |
| | USA | 10 | Japan | 4 | Sweden | 4 | Ireland | |
| | | | Poland | 4 | | | USA | |
| | | | Spain | 6 | | | | |
| | | | USA | 2 | | | | |

2.4.1. Overall effect size

A random-effects model of meta-analysis was used to determine the grand mean, i.e. the overall effect of forest change on litter decomposition. The random-effects model was selected because studies differed from each other and thus variance must be partitioned into within- and between-studies variance. The restricted maximum likelihood method was used to estimate between-study variance. In this analysis, individual effect sizes (lnR) were weighted by the reciprocal of their variance ($1/V_{InR}$) to account for differences in precision among studies. The mean effect size (lnR) was considered as significantly different from zero if its 95% CL did not include zero (Koricheva et al., 2013). The percentage of total variability that is due to between-study variation rather than sampling error (I^2) was also calculated.

2.4.2. Moderator analyses

The effects of moderators on the magnitude and direction of litter decomposition response to forest change were assessed for subsets of the database according to our questions and available sample size; only moderator levels with at least three case studies were compared (Table 1; Table S1). We used mixed-effects models to compare heterogeneity between (Q_B) and within moderator levels to assess the significance of each categorical moderator (Koricheva et al., 2013). Two moderator levels were significantly different if their 95% CL did not overlap. To facilitate interpretation of the results, the ln-mean effect size was back-transformed into mean effect size and then converted into percentage change in decomposition rate between ALT and NAT streams. To avoid potential non-independence between moderators, their effects were tested hierarchically. Interactions between moderators were assessed by the log-likelihood ratio test.

Weighted regressions were used to assess the relationship between the effect of the replacement of native forests by eucalyptus plantations on litter decomposition (lnR) and the ratio of DIN and P concentration between ALT and NAT streams (lntransformed).

2.4.3. Publication bias

Evidence of publication bias in the overall database was assessed by the funnel plot. The 'trim and fill' method was used to assess the impact the publication bias might have on the overall effect size (Jennions et al., 2013). Evidence of publication bias in the subsets used in moderator analyses was assessed by the Rosenberg's fail-safe number (Nfs); when the Nfs number is higher than the threshold value given by $5 \times n + 10$, n = number of effect sizes, the grand mean effect size can be considered robust to publication bias (Jennions et al., 2013).

2.4.4. Sensitivity analysis

Decomposition rates and/or SD had to be estimated for 57 case studies (37% of the total number of case studies; Table S1), which might have biased our results. Thus, we carried out a sensitivity analysis by removing these cases from the database and repeating the analyses. We also repeated the analyses without case studies originating from the pan-European RivFunction project. In this project, a common methodology was used to compare litter decomposition in streams flowing through native and altered forests across Europe (http://webftp.omp.obs-mip.fr/rivfunction/), which contributed 79 case studies to the database (51% of the total number of case studies; Table S1). Also, since using several cases derived from the same study might have biased our results, we repeated the analyses using a mean effect size per study, which was calculated as the weighed mean effect size of all cases considered within that study using mixed-effects model.

3. Results

3.1. Overview of studies

The earliest study that satisfied all our inclusion criteria was published in 1993 (Pozo, 1993). Since then, studies comparing litter decomposition in streams flowing through native and altered forests have been accumulating at a rate of ca. 1 per year (1993–2015); however, in the period 2010–2015, this rate has increased to 1.8 studies per year.

The most commonly studied type of forest change was the replacement of native forests by eucalyptus plantations (42% of studies; 59% of cases) followed by replacement of native forests by conifer plantations (21% of studies; 17% of cases), deciduous plantations (17% of studies, 13% of cases) and the invasion of native forests by exotic woody species (21% of studies, 11% of cases) (Fig. 1, Table S1).

3.2. Overall effect of forest change on litter decomposition in streams

The grand mean effect size lnR was -0.20 (95% CL: -0.28 to -0.12), which corresponds to a significant inhibition of decomposition rate by 18% with forest change (Fig. 1). This estimate is,

however, conservative since 29 missing cases were detected by the 'trim and fill' method to the left of the mean effect size (Fig. S1). After these 29 cases were added to the analysis, the new grand mean effect size lnR was -0.34 (95% CL: -0.43 to -0.25) suggesting an even stronger negative effect (-29%) of forest change on litter decomposition. The Rosenberg's Nfs for the overall database is 10,592, which is 13-fold above the threshold of 790 ($5 \times n + 10$) needed to consider the mean effect size robust. The Nfs for subsets used in moderator analyses were also generally above the threshold, except when mentioned otherwise. Between-study variation explained 96% of the observed variation in the magnitude of the effect. We therefore proceeded to explore the possible causes of this heterogeneity.

3.3. Effects of type of forest change on litter decomposition in streams

The replacement of native forests by eucalyptus and deciduous plantations significantly inhibited litter decomposition rates (by 22% and 26%, respectively), while the replacement of native forests by conifer plantations or the invasion of native forests by exotic woody species had no significant effect on decomposition rates (Fig. 2). Significant differences among types of forest change were found only between deciduous and conifer plantations and between eucalyptus and conifer plantations, with the effect of species invasion not significantly differing from any other type of forest change ($Q_B = 6.419$, df = 3, p = 0.093).

3.4. Replacement of native broadleaf forests by eucalyptus plantations

The replacement of native broadleaf forests by eucalyptus plantations significantly inhibited litter decomposition rates only when the plantations were present at both catchment and riparian areas (-27%) and when native litter was replaced with eucalyptus litter at the stream level (-46%), but not when eucalyptus plantations were present only in the catchment or only in the riparian area (Fig. 3). However, differences among effects of different extents of change were significant only between stream and riparian ($Q_B = 8.831$, df = 3, p = 0.032; Fig. 3). Further analyses excluded cases were litter origin was manipulated ('stream' cases).

Eucalyptus plantations significantly inhibited the decomposition of leaf litter (-26%) but not that of litter mixtures or wood ($Q_B = 6.636$, df = 2, p = 0.036, Fig. 3). Significant differences in effect sizes were found only between leaves and mixtures, as the low sample size for wood likely precluded differences from becoming

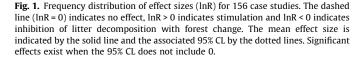
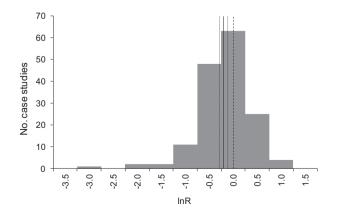
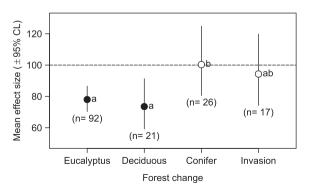


Fig. 2. Effect of four types of forest change on litter decomposition. The dashed line (mean effect size = 100%) indicates no effect, mean effect size > 100% indicates stimulation and mean effect size < 100% indicates inhibition of litter decomposition with forest change. The effect of forest change is significant when the 95% CL does not overlap 100% (black circles). Types of forest change with the same letter do not significantly differ in their effect on litter decomposition. Values in parenthesis indicate the sample size.





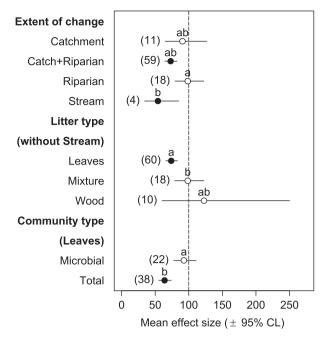


Fig. 3. Effect of the replacement of native broadleaf forests by eucalyptus plantations on litter decomposition as a function of the extent of change, litter type and community type (moderators indicated in bold; subsets of the database used indicated in parenthesis) (see Table S2 for the description of moderators). The dashed line (mean effect size = 100%) indicates no effect, mean effect size > 100% indicates stimulation and mean effect size < 100% indicates inhibition of litter decomposition with forest change. The effect of the replacement of native forests by eucalyptus plantations is significant when the 95% CL does not overlap 100% (black circles). For each moderator, levels with the same letter do not significantly differ in their response to forest change. Values in parenthesis indicate the sample size.

significant (Fig. 3). Further analyses were performed only for leaves.

The effect of eucalyptus plantations on the decomposition of leaf litter strongly depended on the type of decomposer community (Q_B = 9.963, df = 1, p = 0.002), with total leaf litter decomposition being significantly inhibited (-36%), while microbial-driven leaf litter decomposition was not significantly affected (Fig. 3).

When total leaf litter decomposition was considered, significant negative effects of eucalyptus plantations were found for decomposition of litter from the native broadleaf genera (*Alnus*: -51%; *Castanea*: -39%; *Quercus*: -27%), while no significant effect was found for *Eucalyptus* leaves (Fig. 4). However, significant differences were found only between *Alnus* and *Eucalyptus* ($Q_B = 6.062$, df = 3, p = 0.109; Fig. 4). The replacement of native forest by eucalyptus plantations did not significantly affect leaf litter decomposition carried out by microbes of either *Alnus* or *Quercus* ($Q_B = 0.104$, df = 1, p = 0.747; Fig. 4). The interaction between leaf litter identity (*Alnus* and *Quercus*) and community type (microbial and total) was not significant (p = 0.182).

The eucalyptus plantations caused similar degree of inhibition in total leaf litter decomposition in Portugal (-38%) and Spain (-35%) ($Q_B = 0.099$, df = 1, p = 0.753; Fig. 4). Eucalyptus plantations significantly inhibited leaf litter decomposition carried out by microbes in Portugal (-13%) but not in Spain, although the difference between countries was not significant ($Q_B = 1.797$, df = 1, p = 0.180; Fig. 4). The interaction between leaf litter identity (*Alnus* and *Quercus*) and country (Portugal and Spain) was not significant (p = 0.224).

The effect of eucalyptus plantations on litter decomposition did not depend on the nutrient concentrations in the water as no significant relationship was found between the effect size lnR and the ratio in DIN or P concentration between streams flowing through

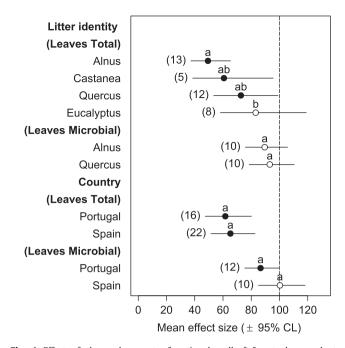


Fig. 4. Effect of the replacement of native broadleaf forests by eucalyptus plantations on litter decomposition as a function of litter identity and country (moderators indicated in bold; subsets of the database used indicated in parenthesis) (see Table S2 for the description of moderators). The dashed line (mean effect size = 100%) indicates no effect, mean effect size > 100% indicates stimulation and mean effect size < 100% indicates inhibition of litter decomposition with forest change. The effect of the replacement of native forests by eucalyptus plantations is significant when the 95% CL does not overlap 100% (black circles). For each moderator, levels with the same letter do not significantly differ in their response to forest change. Values in parenthesis indicate the sample size.

native forests and eucalyptus plantations (p = 0.163 and 0.701, respectively).

3.5. Replacement of native deciduous broadleaf forests by deciduous broadleaf plantations

The replacement of native deciduous broadleaf forests by deciduous broadleaf plantations, mostly beech *Fagus sylvatica*, did not significantly affect microbial-driven or total leaf litter decomposition and no significant differences were found between microbial-driven and total decomposition ($Q_B = 0.251$, df = 1, p = 0.616; Fig. 5). Deciduous plantations significantly inhibited the decomposition of *Quercus* leaves (-45%), but not of *Alnus* leaves, although the difference between litter genera was not significant ($Q_B = 2.730$, df = 1, p = 0.098; Fig. 5). The interaction between leaf litter identity (*Alnus* and *Quercus*) and community type (microbial and total) was not significant (p = 0.158).

3.6. Replacement of native deciduous broadleaf forests by conifer plantations

The overall effect of the replacement of native deciduous broadleaf forests by conifer plantations on litter decomposition was not significant (R = 100%, 95% CL: 81–125%). However, the effect of conifer plantations on litter decomposition depended on the extent of forest change ($Q_B = 5.983$, df = 1, p = 0.014), with significant negative effects observed when the replacement of native deciduous broadleaf forests by conifer plantations was done at the catchment level (-31%; R = 69%, 95% CL = 48–99%), but no effects when the plantations were present in both the catchment and the riparian area (14%; R = 114%, 95% CL = 95–139%). The potential effect of conifer species in plantations and region (country) on the response of litter

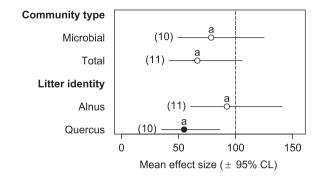


Fig. 5. Effect of the replacement of native deciduous broadleaf forests by deciduous broadleaf plantations on litter decomposition as a function of community type and litter identity (see Table S2 for the description of moderators). The dashed line (mean effect size = 100%) indicates no effect, mean effect size > 100% indicates stimulation and mean effect size < 100% indicates inhibition of litter decomposition with forest change. The effect of the replacement of native forests by deciduous plantations is significant when the 95% CL does not overlap 100% (black circles). For each moderator (indicated in bold), levels with the same letter do not significantly differ in their response to forest change. Values in parenthesis indicate the sample size.

decomposition to forest change could not be assessed as these variables were correlated (Table S1). The effect of conifer plantations on litter decomposition did not depend on litter identity when plantations were either in the catchment ($Q_B = 0.888$, df = 1, p = 0.346) or in both the catchment and the riparian area ($Q_B = 0.046$, df = 1, p = 0.830), but these results are not robust to possible publication bias (n = 6, Nfs = 12 and n = 12, Nfs = 0, respectively).

3.7. Invasions of native forests by exotic woody species

Invasion of native forests by exotic woody species did not significantly affect litter decomposition (R = 106%, 95% CL: 74– 120%). This is likely due to contrasting effects of different invasive species on litter decomposition. However, identity of invasive species was correlated with country which precluded the analysis (Table S1). There was, nevertheless, no significant effect of litter origin (native or exotic) on the response of litter decomposition to species invasion ($Q_B = 0.360$, df = 1, p = 0.548). Also, no significant effect of the type of native forest (deciduous broadleaf or eucalyptus forest; $Q_B = 0.031$, df = 1, p = 0.860) or of litter identity ($Q_B = 3.157$, df = 2, p = 0.206) was found, but these results are not very robust to possible publication bias (n = 15, Nfs = 75 and n = 9, Nfs = 0, respectively).

3.8. Sensitivity analyses

Repeating the analyses without estimated cases or cases originating from the RivFunction project did not change our results and interpretations much (Tables S3 and S4). When a single combined effect size per study was used, the overall effect of forest change on litter decomposition remained significant and was not affected by publication bias. The effect of the replacement of native deciduous broadleaf forest by deciduous broadleaf plantations on litter decomposition was not significant, likely due to low number of effect sizes now considered (n = 4) and contrasting responses of different litter species or community types (microbes vs. microbes + invertebrates) to forest change within each study (Table S5).

4. Discussion

4.1. Overall effect of forest change on litter decomposition in streams

Our systematic review of the effect of the replacement of native forests by tree plantations or invasion by exotic woody species on litter decomposition in streams showed that forest change significantly inhibited litter decomposition by 18%. Our results are robust to publication bias as indicated by the Rosenberg fail safe numbers. However, they might be conservative as the 'trim and fill' method suggests an even stronger negative effect of forest change on liter decomposition (-29%). Although our database consisted of 156 effect sizes derived from 24 studies, our results are not strongly affected by the non-independence of multiple effect sizes per study as indicated by sensitivity analysis.

The evaluation of the effects of the replacement of native forests by tree plantations or invasion by exotic woody species on litter decomposition in streams by comparing streams flowing through native and altered forests started recently; the oldest study included in this review dates from 1993 (Pozo, 1993). The rate at which studies have accumulated has increased over the last 5 years considered in this review (2010–2015), which reflects an increase in the interest of researchers by this subject, likely motivated by the awareness that many streams worldwide now flow through altered forests (Kominoski et al., 2013).

4.2. Replacement of native broadleaf forests by eucalyptus plantations

As expected, the replacement of native broadleaf forests by Eucalyptus globulus plantations significantly inhibited litter decomposition (-22%) since eucalyptus plantations lead to strong changes in litter inputs to streams as well as in stream hydrology (Graça et al., 2002). Litter inputs to streams flowing through eucalyptus plantations are dominated by eucalyptus litter (Pozo et al., 1997; Molinero and Pozo, 2006; Laćan et al., 2010), which has low nutrient concentration, high concentration of secondary compounds (e.g. essential oils, polyphenolics) and a thick and waxy cuticle (Bärlocher et al., 1995; Pozo et al., 1998; Canhoto and Graça, 1999). This is a poor substrate for stream detritivores (Canhoto and Graça, 1995) and may limit their populations. In addition, Abelho and Graça (1996) suggested that the release of oils by eucalypt litter results in hydrophobic soils with consequent changes in hydrology (more frequent spates and intermittency) which further limit detritivores populations. In fact, low diversity and biomass of invertebrates in streams flowing through eucalyptus plantations compared with streams flowing through native forests were reported before (Abelho and Graça, 1996; Larrañaga et al., 2009a,b).

The magnitude of the effect of eucalyptus plantations on litter decomposition depended, however, on whether tree plantations reached the riparian zone. Litter decomposition was significantly inhibited when eucalyptus plantations were reaching the stream banks (-27%), suggesting that the effects of eucalyptus plantations on stream functioning are mediated by changes in both litter input (stronger when forest change occurs in the riparian area) and stream hydrology (stronger when forest change occurs in the catchment area). The presence of a buffer zone of native deciduous species when plantations occur at the catchment level likely mitigated the potential negative effects of eucalyptus plantations on aquatic communities and processes (Ormerod et al., 1993; Broadmeadow and Nisbet, 2004). The only study of effects of the presence of eucalyptus trees at the riparian area only (Laćan et al., 2010) reported no major effects on litter decomposition, despite changes in litter inputs to streams. In the latter study, however, the native forest was mostly evergreen and there was no major change in the phenology of litter inputs to streams when it was replaced by eucalyptus (Lacan et al., 2010). The replacement of native deciduous litter inputs by eucalyptus litter inputs in a manipulative experiment at the stream reach level (Larrañaga et al., 2014) also resulted in a strong inhibition of litter decomposition (-46%), which supports the suggestion that effects of eucalyptus plantations on litter decomposition are strongly mediated through changes in litter inputs.

Eucalyptus plantations significantly inhibited decomposition of leaves (-26%), while the decomposition of woody substrates was not significantly affected, which was anticipated. Also according with predictions, there was a tendency for stronger inhibition of total decomposition of more labile leaves as compared to more recalcitrant leaves: *Alnus* (-51%) > *Castanea* > *Quercus* > *Eucalyptus* (-17%). This suggests that eucalyptus effects on litter decomposition are mediated through effects on macroinvertebrates since the contribution of invertebrates to litter decomposition is generally higher for high quality (soft, low C:nutrients ratios) than for low quality litter (Hieber and Gessner, 2002; Gulis et al., 2006). Also, taxa richness and density of total macroinvertebrates were lower in streams flowing through eucalyptus plantations than in those flowing through native deciduous forests in Central Portugal (Abelho and Graca, 1996). Recent studies in Spanish Atlantic streams have also found lower taxa richness, density and biomass of total macroinvertebrates and detritivores, mostly of large detritivore taxa as Echinogammarus spp. and Limnephilidae caddisflies, in streams flowing through eucalyptus plantations than in those flowing through native deciduous forests (Larrañaga et al., 2009a). These differences in invertebrate parameters between stream types likely result from changes in seasonality and quality of litter inputs to streams and changes in hydrology (Abelho and Graça, 1996; Larrañaga et al., 2009a).

Microbial communities, on the other hand, are considered more redundant and thus changes in their community structure may not translate into effects on ecosystem processes (Bärlocher and Graça, 2002; Dang et al., 2005; Ferreira et al., 2006). For instance, aquatic hyphomycete species richness and evenness were lower in streams flowing through eucalyptus plantations than in streams flowing through native deciduous forests in Central Portugal, but this did not translate into differences in decomposition rates of chestnut and eucalyptus litter between stream types (Bärlocher and Graça, 2002). In addition, fungal biomass on decomposing alder and oak leaves was higher in streams in eucalyptus plantations than in streams in deciduous forests, and aquatic hyphomycetes community structure on leaves differed between stream types, but this did not translate into differences in litter decomposition rates between streams in Central Portugal and Northern Spain (Ferreira et al., 2006, 2015). Conidial production, species richness and diversity of aquatic hyphomycetes may not even significantly differ between eucalyptus and deciduous streams as found by Chauvet et al. (1997) in Spanish Atlantic streams.

The mediation of the eucalyptus effects on litter decomposition by changes in invertebrate community structure/activity is further supported by the significant inhibition of total leaf litter decomposition by forest change (-36%), while microbial-driven leaf litter decomposition was not significantly altered. However, generally decomposition experiments terminate at the same time for coarse (total litter decomposition) and fine mesh bags (microbial-driven litter decomposition) and thus microbial-driven litter decomposition is at a less advanced stage than total litter decomposition. We do not know whether, if fine mesh bags would be allowed to remain in the streams for longer periods, the effects of eucalyptus plantations would be revealed also for microbial-driven litter decomposition. Results so far indicate that the replacement of native forests by eucalyptus plantations may have more negative effects in streams that receive natural high quality litter and where invertebrate detritivores play an important role on ecosystem functioning.

The replacement of native deciduous broadleaf forests by eucalyptus plantations significantly inhibited total leaf litter decomposition in Portugal and Spain to the same degree (-38% and -35%, respectively). On the contrary, the effect of eucalyptus plantations on microbial-driven leaf litter decomposition was significant for Portugal (-13%) but not for Spain, although differences between countries were not significant. We expected that the effect of eucalyptus plantations on litter decomposition in streams would be stronger in drier regions (e.g. central Portugal) than in more humid regions (e.g. northern Spain), as streams flowing through eucalyptus plantations in drier regions would likely dry out during the warmer months, which has negative effects on aquatic communities (Datry et al., 2011). Stronger effects of eucalyptus plantations on the community structure of aquatic hyphomycetes associated with decomposing litter and on benthic invertebrates density have been found in central Portugal than in northern Spain (Ferreira et al., 2006, 2015). However, these differences in the response of aquatic communities to eucalyptus plantations did not translate into strong differences in the response of litter decomposition to eucalyptus plantations between countries, which suggests some degree of functional redundancy in aquatic communities or changes in other variables that may mitigate the effect of eucalyptus plantations on litter decomposition in Portuguese streams. If streams flowing through eucalyptus plantations would have higher dissolved nutrient availability, this could counteract to some degree the inhibitory effect of eucalyptus plantations on litter decomposition due to a stimulation of microbial conditioning. However, no relationship was found between the response of litter decomposition to eucalyptus presence and the ratio of dissolved nitrogen or phosphorus between altered and reference streams.

Although the eucalyptus subset was the largest subset in our review (42% of studies; 59% of cases), it did not cover the variety of conditions in which eucalyptus plantations are replacing native forests worldwide. The studies included in our review were carried out mainly in the Iberian Peninsula, but Eucalyptus plantations cover > 20 million ha in over 65 countries, across a range of climate conditions (Iglesias-Trabado et al., 2009). China, India and Brazil hold > 50% of global eucalyptus plantations (Iglesias-Trabado et al., 2009) and thus the lack of primary studies addressing the effects of eucalyptus plantations on litter decomposition in streams in these countries is surprising. Eucalyptus species in plantations also differ among regions (e.g. E. globulus in the Iberian Peninsula and Eucalyptus grandis in Brazil), as do the native forests they replace (e.g. mixed deciduous broadleaf forests in the Iberian Peninsula, Cerrado in Brazil, evergreen broadleaf forests in China). This highlights the need for primary studies addressing the effects of eucalyptus plantations on stream ecosystem processes across the range of conditions where they occur.

4.3. Replacement of native deciduous broadleaf forests by deciduous broadleaf plantations

The replacement of native deciduous broadleaf forests by deciduous broadleaf plantations significantly inhibited litter decomposition (-26%). In most cases (20 out of 21), native forests were replaced by F. sylvatica plantations (Lecerf et al., 2005; Lecerf and Chauvet, 2008; Hladyz et al., 2011a), which resulted in a decrease in diversity of litter inputs to streams (Lecerf et al., 2005). Streams receiving low species richness litter inputs have low fungal species richness (e.g. Laitung and Chauvet, 2005). Also, F. sylvatica litter has poor nutritional quality (Gessner and Chauvet, 1994; Bruder et al., 2014). As a result, it may support lower microbial production than other deciduous litter species (Gessner and Chauvet, 1994), while benthic invertebrates are not strongly affected (Bruder et al., 2014). The stronger effect of F. sylvatica plantations on microbial than on invertebrate communities may explain the significant negative effect of forest change on the decomposition of low quality litter (*Quercus robur*, -45%), while the decomposition of high quality litter (A. glutinosa) was not significantly affected. Studies on the effects of replacement of native forests with other deciduous plantations (e.g. *Platanus hybrida*, *Populus* sp.) on litter decomposition in streams are, however, scarce (but see Menéndez et al., 2013).

4.4. Replacement of native deciduous broadleaf forests by conifer plantations

Contrary to expectations, the replacement of native deciduous broadleaf forests by conifer plantations did not have a significant effect on litter decomposition in streams. Although the annual litter input may not significantly differ between native broadleaf forests and conifer plantations, its phenology and composition are drastically altered (Stefánsdóttir, 2010; Inoue et al., 2012; Martínez et al., 2013). Needles, which dominate in litter inputs to streams flowing through conifer plantations, have low nutrient concentration, high concentration of secondary compounds and are tough (Gunasekera and Webster, 1983; Martínez et al., 2013, 2015), making them poor food sources for decomposers (Friberg and Jacobsen, 1994). Also, streams flowing through conifer plantations are often acidic, which could be less favorable for aquatic biota (Ormerod et al., 1989; Cannell, 1999). Nevertheless, despite changes in shredder community structure, there seems to be a certain level of functional redundancy as this not always translates into changes in decomposition rates (Riipinen et al., 2010; Hisabae et al., 2011). The absence of an overall effect of conifer plantation on litter decomposition might also be attributed to distinct effects of the different conifer species on stream communities, which was not possible to assess due to covariation between conifer species and country and low sample size.

The effect of conifer plantations on litter decomposition was, however, dependent on the extent of forest change, as the replacement of native forests by conifer plantations at the catchment level significantly inhibited litter decomposition (-31%) whereas its replacement by plantations at the catchment plus riparian area did not have a significant effect. This result is contrary to our predictions and may have been confounded by low number of case studies reporting forest replacement at the catchment only (n = 6) and/or by the fact that all these cases originated from a single primary study (Martínez et al., 2013). In this study, the replacement of native deciduous forests by Pinus radiata plantations at the catchment level in northern Spain negatively affected the density, richness and diversity of aquatic shredders, which translated into inhibition of litter decomposition rates (Martínez et al., 2013). Kominoski et al. (2011) assessed litter decomposition and associated decomposers in streams flowing through conifer forests with different riparian tree species composition, varying from mostly conifer (dominated by hemlock Tsuga heterophylla) to mostly deciduous (dominated by red alder Alnus rubra). They found a significant positive relationship between total red alder decomposition rates and percentage deciduous riparian canopy cover (Kominoski et al., 2011). This is consistent with our results where the replacement of native deciduous broadleaf forests by conifer plantations affected litter decomposition only when deciduous tree species were still present in the riparian area (Martínez et al., 2013), although in the opposite direction to that observed by Kominoski et al. (2011). In the study by Kominoski et al. (2011), the relationship between total red alder decomposition rates and deciduous riparian cover was also likely mediated by differences in macroinvertebrates biomass and abundance associated with decomposing litter.

Conifer plantations are the most common plantations worldwide, but only five studies have so far addressed the effects of the replacement of native forests by these plantations on litter decomposition in streams. This paucity of studies represents a gap in our knowledge of the effects of conifer plantations on stream ecosystem functioning and hinders the development of management recommendations.

4.5. Invasions of native forests by exotic woody species

Invasions of native forests by exotic woody species did not have a significant effect on litter decomposition in streams, which can be due to low number of available studies (n = 4) and/or contrasting effects of the different invasive species on stream communities. Studies addressing the effect of the invasion of native deciduous forests by Rhododendron ponticum in Ireland (Hladyz et al., 2011b), Tamarix ramossisima in USA (Kennedy and Hobbie, 2004) or Prunus padus in Alaska (Roon et al., 2014) reported inhibition of litter decomposition, while studies addressing the effect of the invasion of native deciduous forests by Fallopia japonica in France and England (Lecerf et al., 2007) or of native Eucalyptus camaldulensis forests by Salix babylonica in Australia (Schulze and Walker, 1997) generally report stimulation of or no effect on litter decomposition. It was not possible, however, to test the effect of invasive species identity on litter decomposition as it covaried with country and sample size was small. Invasion of riparian areas by exotic species is common worldwide and is predicted to continue in the future as a result of human-induced disturbance and climate change (Dukes and Mooney, 1999; Catford et al., 2013; Kominoski et al., 2013). Although we should not 'judge species on their origins' (Davis et al., 2011), invasive species have the potential to alter stream ecosystem functioning through multiple pathways. Invasive species may alter the quality of litter inputs by contributing directly to the litter pool and/or by changing native species litter quality (e.g. when nitrogen-fixing invasive species lead to increases in the nitrogen concentration in native species) or quantity (Arthur et al., 2012; Millett et al., 2012). Invasive species may also alter dissolved nutrient concentrations due to the decomposition of changed litter inputs and/or through leaching from the soil, especially when the proportion of nitrogen-fixers shifts (Goldstein et al., 2009; Mineau et al., 2011; Wiegner et al., 2013). Thus, more primary studies on the impacts of invasive species on litter decomposition are urgently needed to increase our understanding of the effects of invasive plant species on aquatic communities and ecosystem processes and to better identify its moderators, which is essential for the development of appropriate mitigation measures.

4.6. Forecasting litter decomposition responses based on plant trait similarity between native and altered forests

Our results give some support to the conceptual framework proposed by Kominoski et al. (2013), which predicts responses of stream communities and processes to shifts in riparian plant species based on species traits similarity. As expected, we found a significant response of litter decomposition to the replacement of native deciduous, but not evergreen forests by *E. globulus*. Dominant trees in native deciduous forests (e.g. oak *Q. robur*, chestnut *Castanea sativa*) and riparian areas (e.g. alder *A. glutinosa*) are slow growing, shed their leaves in autumn/winter and have higher leaf litter quality than *E. globulus*, which is a fast growing, evergreen species (Graça et al., 2002). These, and other, differences in species traits lead to differences in aquatic communities and litter decomposition between streams flowing though native deciduous broadleaf forests and *E. globulus* plantations, as discussed above.

Based on the same premise, we would expect a significant response of litter decomposition to the replacement of native deciduous broadleaf forests by conifer plantations (Kominoski et al., 2013). This was not the case, although conifer needles are generally regarded as being of worse nutritional quality for decomposers than leaves from most broadleaf species. However, each study considered a different native broadleaf forest-conifer plantation pair and this might have confounded the results. The replacement of native deciduous broadleaf forests by deciduous plantations does not necessary lead to a change in tree species traits, since the species most often used in the deciduous plantations considered (*F. sylvatica*) is often also present in native forests. However, the replacement of diverse native forests by a tree monoculture leads to a decrease in the diversity of plant traits, which is likely to have a negative effect on communities and ecosystem functioning (Kominoski et al., 2013). Our results agree with this prediction as litter decomposition was inhibited by the replacement of native deciduous broadleaf forests by singlespecies deciduous plantations.

The invasion of native forests by low to moderate densities of exotic tree species may increase plant trait diversity, while their dominance by exotic species will lead to a decrease in plant trait diversity. Both situations can affect stream communities and processes (Kominoski et al., 2013). However, we did not find a significant effect of invasion of native forests by exotic species on litter decomposition, which might be attributed to different native forests-exotic species pairs and to different intensity of species invasion considered across studies.

4.7. Comparison of streams flowing through native versus altered forests and comparison of native versus exotic litter

Large areas of native forests are being replaced by tree plantations or invaded by exotic woody species worldwide (Dukes and Mooney, 1999; Catford et al., 2013; Kominoski et al., 2013), which can potentially affect stream communities and processes (Gessner and Chauvet, 2002; Young et al., 2008). However, only 24 primary studies addressing the effects of forest change on the decomposition of natural allochthonous litter in streams have been conducted so far and were included in this review. This contrasts with numerous studies assessing the decomposition of native versus exotic litter under laboratory conditions or in single stream conditions (e.g. Albariño and Balseiro, 2002; Reinhart and VandeVoort, 2006; Braatne et al., 2007; Moline and Poff, 2008; Raposeiro et al., 2014). Although such studies provide a useful insight on how aquatic communities may respond to the presence of exotic litter, they cannot inform us about the way aquatic communities and processes will respond to forest change. When comparing decomposition rates between native and exotic litter, we are addressing only the effect of litter quality (i.e. physical and chemical characteristics) on a process (which reflects community performance, or individual performance in the case of most laboratory experiments), while the replacement of native forests by tree plantations or invasion by exotic species leads to more than just changes in the quality of the litter inputs (Graça et al., 2002; Mineau et al., 2011). Only by comparing litter decomposition in streams flowing through native forests versus streams flowing through altered forests will it be possible to assess the response of stream ecosystem functioning to forest change, taking into account the changes in quality, quantity, phenology and diversity of the litter input as well as changes in hydrology and water quality introduced to the system, and that likely lead to changes in the aquatic communities that mediate the decomposition of allochthonous litter and its incorporation into the food web.

5. Conclusion

We found that there is an overall inhibition of litter decomposition with forest change and that the significance of this effect depends on the type of forest change, extent of change, identity of the decomposing litter and type of decomposer community. Thus, predictions of the effects of forest change on stream functioning need to take into account multiple factors besides the identity of the species in plantations.

The significant inhibition of litter decomposition when eucalyptus plantations were present in both the catchment and the riparian area, but not when plantations were present only in the catchment, suggests that the presence of native tree species in the riparian area may mitigate the negative effects of eucalyptus plantations on stream processes. Thus, an effort should be made to preserve or restore native riparian areas in streams flowing through eucalyptus plantations. The existence of a riparian area of native species is especially important if native species produce soft, high quality litter and if detritivores play an important role in stream processes since the decomposition of high quality litter in the presence of detritivores was the most strongly inhibited by eucalyptus plantations.

Important gaps still exist in primary research, which limits management recommendations. First, further research on the effects of forest change on stream functioning should compare streams flowing through native forests versus streams flowing through altered forests in order to capture the overall effects of forest change (not only those mediated through differences in litter characteristics) on litter decomposition. Second, studies addressing the effects of eucalyptus plantations in tropical regions are necessary as climate, eucalyptus species and native forests differ from those in the Iberian Peninsula and thus the recommendations made above may not hold true in these regions. Third, more studies are needed on the effects of conifer plantations and deciduous plantations as variability in results is presently high and potentially due to differences in climate and species identity among studies. Finally, invasion of riparian forests by exotic species is a serious problem worldwide and will continue to be so in the future due to climate change and human activities that facilitate the transport of exotic species and promote disturbance that facilitates their establishment. Thus, it is urgent to amplify our understanding of the effects of invasion by exotic species on stream functioning. This is presently limited by the small sample size associated with each exotic species, which covaried with location.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2016.01. 002.

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