Invasion of temperate deciduous broadleaf forests by N-fixing tree species – consequences for stream ecosystems

Verónica Ferreira¹,*, Albano Figueiredo², Manuel A. S. Graça¹, Elizabete Marchante³ and Ana Pereira¹

¹University of Coimbra, MARE – Marine and Environmental Sciences Centre, Department of Life Sciences, Calçada Martim de Freitas, 3000–456, Coimbra, Portugal

²University of Coimbra, CEGOT – Centre for Studies in Geography and Spatial Planning, Department of Geography and Tourism, Largo da Porta Férrea, 3004–530 Coimbra, Portugal

³University of Coimbra, CFE – Centre for Functional Ecology, Department of Life Sciences, Calçada Martim de Freitas, 3000–456 Coimbra, Portugal

⁎Author for correspondence (Tel.: +351 918 435 396; E-mail: veronica@ci.uc.pt).

ABSTRACT

Biological invasions are a major threat to biodiversity and ecosystem functioning. Forest invasion by alien woody species can have cross-ecosystem effects. This is especially relevant in the case of stream–riparian forest meta-ecosystems as forest streams depend strongly on riparian vegetation for carbon, nutrients and energy. Forest invasion by woody species with dissimilar characteristics from native species may be particularly troublesome. The invasion of temperate deciduous broadleaf forests with low representation of nitrogen (N)-fixing species by N-fixers has the potential to induce ecosystem changes at the stream level. Although effects of tree invasion on stream ecosystems have been under assessed, knowledge of native and invasive tree characteristics allows prediction of invasion effects on streams. Here we present a conceptual model to predict the
effects of forest invasion by alien N-fixing species on streams, using as a background the invasion of temperate deciduous broadleaf forests by leguminous *Acacia* species, which are among the most aggressive invaders worldwide. Effects are discussed using a trait-based approach to allow the model to be applied to other pairs of invaded ecosystem–invasive species, taking into account differences in species traits and environmental conditions. Anticipated effects of N-fixing species invasions include changes in water quality (increase in N concentration) and quantity (decrease in flow) and changes in litter input characteristics (altered diversity, seasonality, typology, quantity and quality). The magnitude of these changes will depend on the magnitude of differences in species traits, the extent and duration of the invasion and stream characteristics (e.g. basal nutrient concentration). The extensive literature on effects of nutrient enrichment of stream water, water scarcity and changes in litter input characteristics on aquatic communities and processes allows prediction of invasion effects on stream structure and function. The magnitude of invasion effects on aquatic communities and processes may, however, depend on interactions among different pathways (e.g. effects mediated by increases in stream nutrient concentration may contrast with those mediated by decreases in water availability or by decreases in litter nutritional quality). A review of the literature addressing effects of increasing cover of N-fixing species on streams suggests a wide application of the model, while it highlights the need to consider differences in the type of system and species when making generalizations. Changes induced by N-fixing species invasion on streams can jeopardize multiple ecosystem services (e.g. good quality water, hydroelectricity, leisure activities), with relevant social and economic consequences.

**Key words:** *Acacia*, alien tree species, conceptual model, forest change, litter decomposition, stream communities.
II. Case studies of increasing cover by N-fixing species
III. The invasion of temperate deciduous broadleaf forests by Acacia species
   (1) Temperate deciduous broadleaf forests and their streams
   (2) Invasive behaviour of Acacia species
   (3) Streams as invasion corridors
   (4) Invasion of temperate deciduous broadleaf forests by Acacia species in Portugal
IV. Anticipated effects of Acacia invasion of riparian areas on streams – a conceptual model
   (1) Changes in water quality
   (2) Changes in water quantity
   (3) Changes in litter inputs to streams
      (a) Changes in the diversity of litter inputs
      (b) Changes in the phenology of litter inputs
      (c) Changes in the typology of litter inputs
      (d) Changes in the quantity of litter inputs
      (e) Changes in the quality of litter inputs
      (f) Changes in allelopathic compounds
   (4) Changes in stream litter decomposition and aquatic communities
      (a) Response to changes in water quality
      (b) Response to changes in water quantity
      (c) Response to changes in litter input characteristics
V. Conceptual framework to predict effects of invasion of riparian areas by N-fixing species on
   streams
VI. Decomposition of Acacia leaf litter in streams
VII. Impacts of invasive N-fixing species on ecosystem services provided by streams
VIII. Future directions
IX. Conclusions
I. INTRODUCTION

Biological invasions are a major threat to ecosystems worldwide, leading to changes in community structure, which can result in biodiversity loss and impairment of ecosystem functioning (Vitousek et al., 1997; Gallardo et al., 2016; Vilà & Hulme, 2017; Brondízio et al., 2019). Invasions by alien species are so widespread (Early et al., 2016), that since the 1990s they have become “a significant component of human-caused global change” (Vitousek et al., 1997, p. 1). Biological invasion effects are generally studied from the perspective of the invaded ecosystem. However, invasions may trigger cross-ecosystem effects, which are addressed less often (but see e.g. Baxter et al., 2004; Hladyz et al., 2011; McNeish, Benbow & McEwan, 2012). This is particularly true in the case of stream–riparian forest meta-ecosystems. The invasion of riparian forests by alien woody species can deeply affect their biodiversity and functioning (Urgenson, Reichard & Halpern, 2009; Tererai et al., 2013; Gutiérrez-López et al., 2014; Constán-Nava et al., 2015), but it can also affect stream ecosystems given their large aquatic–terrestrial interface and strong dependency on riparian vegetation (Lecerf et al., 2007; Atwood et al., 2010; Hladyz et al., 2011; Mineau et al., 2012).

Riparian vegetation is one of the most important factors controlling in-stream functioning: it provides shade, thus reducing the amount of solar radiation reaching the stream bed and controlling water temperature, which limits in-stream primary production; it provides organic matter as a food source and substrate for aquatic organisms; it provides habitat for aquatic organisms (e.g. submerged roots, branches and logs); it stabilizes the banks, limiting erosion and the input of fine sediments; and it also buffers the impact of human activities, such as forestry, agriculture or urbanization, on streams (e.g. by reducing the input of nutrients and pesticides) (Cummins et al., 1989; Wenger, 1999; Dosskey et al., 2010; Tolkkinen et al., 2020). However, given their position in the interface between the aquatic and terrestrial environments, riparian forests are one of the most
susceptible habitats to species invasions, especially in landscapes highly disturbed by human activities (Pyšek et al., 2010), and are listed among the most invaded habitats (Richardson et al., 2007). On one hand, stream hydrologic dynamics are, by nature, a source of disturbance for riparian areas (e.g. spates and floods), making them susceptible to invasions (Lewerentz et al., 2019).

Streams can also act as corridors for invasions by carrying plant propagules downstream and sideways (e.g. during floods) (Cabra-Rivas, Alonso & Castro-Díez, 2014; Catford & Jansson, 2014; Kuglerová et al., 2015; Čuda et al., 2017). On the other hand, human activities such as forestry, agriculture and urbanization often compete for space with riparian forests leading to their degradation (Pennington, Hansel & Gorchov, 2010). Additionally, because human activities are the primary cause of the introduction (intentional or accidental) of alien species, the proximity of these activities to riparian forests increases their exposure to biological invasions (Sanz-Elorza, Dana & Sobrino, 2006; Giorgis et al., 2011; Spear et al., 2013).

The effects of invasion by alien riparian tree species on stream ecosystems may be stronger when invasive and native species are functionally different (Kominoski et al., 2013; Castro-Díez et al., 2014; Le Maitre, Gush & Dzikiti, 2015). In particular, the arrival of alien nitrogen (N)-fixing woody species to riparian habitats where this functional trait is underrepresented or absent may have significant effects on stream functioning, as suggested by two meta-analyses on the effects of plant invasions on terrestrial ecosystems (Liao et al., 2008; Castro-Díez et al., 2014). Liao et al. (2008) found stronger influences on N cycles of invasions by N-fixing than by non-N-fixing species and Castro-Díez et al. (2014) found that alien plant invasions alter N cycles especially when invasive and native species differ in their N-fixing ability. The magnitude of the effects may increase with the establishment of monospecific stands of the invasive species, which reduces compositional and functional plant diversity and redundancy (Kominoski et al., 2013), leading to the creation of novel riparian ecosystems (Catford et al., 2013). Also, changes in ecosystem structure and function may be stronger in the case of long-term than more recent invasions (Marchante et al., 2008, 2015; Souza-Alonso, Guisande-Collazo & González, 2015). With invasion...
time, the reversibility of the effects also decreases, making recovery more difficult (Le Maitre et al., 2011).

Invasions by alien N-fixing woody species are a global problem. Richardson & Rejmánek (2011) identified 131 N-fixing tree and shrub species (legumes plus actinorhizal species) that are invasive in at least one region, representing 21% of the total number of invasive alien tree and shrub species worldwide. Castro-Díez & Alonso (2017) listed 12 alien tree species invading riparian areas in the Iberian Peninsula, 50% of which are N-fixing species. Understanding how streams function under invaded riparian forests is crucial to foresee invasion impacts on stream ecosystem services, which are disproportionally numerous and vital taking into account the small area streams occupy globally (Capon et al., 2013). However, despite the high number of invasive alien N-fixing woody species, studies addressing their effects on stream ecosystems are scarce.

II. CASE STUDIES OF INCREASING COVER BY N-FIXING SPECIES

Existing studies have addressed the in-stream effects of invasion by alien species such as Acacia mearnsii in South Africa, Elaeagnus angustifolia in the western USA, Elaeagnus umbellata in the eastern USA, Falcataria moluccana in Hawaii and Ulex europaeus in New Zealand (Table 1). Despite the small number of studies, and differences in the identity and functional type of the invasive species and in the type of the invaded ecosystem, it emerges as a general trend that the invasion of riparian areas by N-fixing species leads to higher N concentrations in stream water and sediments (Goldstein, Williard & Schoonover et al., 2009; Atwood et al., 2010; Mineau, Baxter & Marcarelli, 2011; Wiegner et al., 2013; Stewart et al., 2019) and lower N limitation of biofilms (Mineau et al., 2011; Wiegner et al., 2013). Changes in litter inputs (Mineau et al., 2012; Railoun, 2018), the N cycle (Mineau et al., 2011; Stewart et al., 2019), benthic invertebrate communities (Lowe et al., 2008) and food webs (Atwood et al., 2010) have also been reported (Table 1).

Despite our focus on invasion by alien N-fixing species, studies addressing the colonization and expansion of native N-fixing species are also relevant in the present context. The colonization
of conifer clear-cut areas by the native deciduous N-fixing *Alnus rubra* in western North America has been most studied (Kominoski *et al*., 2013; Table 2). *Alnus rubra* is a fast-growing pioneer species that rapidly colonizes disturbed areas, including riparian areas. As a result, second-growth forests regenerated after timber harvest have a higher proportion of N-fixing trees compared with old-growth forests (Kominoski, Marczak & Richardson, 2011). Colonization by *A. rubra* has been associated with increases in stream water N concentrations (Compton *et al*., 2003; Volk, Kiffney & Edmonds, 2003), although the magnitude of the effect seems to depend on the extent of the colonization with stronger effects when *A. rubra* is present in both the riparian area and the catchment than when it is only in the riparian area (Compton *et al*., 2003; Kominoski *et al*., 2011). Also, because riparian forests are dominated by young-aged stands of *A. rubra*, transpiration is higher than in old-growth conifer forests (Moore *et al*., 2004), which may lead to reductions in stream discharge.

Riparian forests dominated by *A. rubra* contribute greater annual amounts of litter to streams than riparian forests dominated by conifer species, with differences in litter inputs being especially strong in autumn, when *A. rubra* sheds its leaves (Volk *et al*., 2003; Hart, 2006). Since N concentrations of several litter components are higher for riparian forests dominated by *A. rubra* than by conifer species (Volk *et al*., 2003; Hart, 2006), litter N fluxes are higher to streams flowing through the former than the latter forest type (Hart, 2006). Export of detritus to downstream reaches is also higher in streams flowing through riparian areas colonized by *A. rubra* than through old-growth conifer forests (Piccolo & Wipfli, 2002; Wipfli & Musslewhite, 2004), which likely subsidizes downstream food webs. These changes in stream conditions and litter inputs affect aquatic biota and processes (Table 2).

Comparison of studies addressing the increase in cover by N-fixing species (native or alien) suggests that extrapolations to other situations need to consider differences in the invaded systems and invasive species. For instance, effects may differ when conifer forests are colonized or invaded by deciduous N-fixing species (e.g. *A. rubra*) and when deciduous broadleaf forests are colonized...
or invaded by evergreen alien N-fixing species (e.g. *Acacia* species). The large number of invasive and potentially invasive N-fixing species that could significantly change stream–riparian forest meta-ecosystems and the large areas they have already invaded (Richardson & Rejmánek, 2011) make the understanding of their effects urgent. This is especially important given that mitigating N-enrichment of freshwater ecosystems is a major conservation challenge (Vitousek *et al*., 1997; Carpenter, Stanley & Vander-Zanden, 2011), and the effects of invasive N-fixing species have been largely overlooked in this context.

Here, we discuss the potential effects of the invasion of riparian ecosystems by alien N-fixing woody species on stream ecosystems, and propose a conceptual model for predicting such effects. We use as a background the invasion of temperate deciduous broadleaf riparian forests, with reduced representation of native N-fixing species, by *Acacia* species (*Acacia dealbata* and *Acacia melanoxylon*, in particular), as observed in the northwest corner of the Iberian Peninsula (Hernández *et al*., 2014; ICNF, 2019). These invasive alien species are a major threat to deciduous forests on the Iberian Peninsula, but also to forests in other mediterranean-climate regions (e.g. south Europe, South Africa, Chile) (Table 3). Since effects are discussed on the basis of plant traits, the potential effects of invasion by *Acacia* species can likely be extrapolated to other invasive species, taking into account differences in native and invasive species traits and in environmental conditions.

III. THE INVASION OF TEMPERATE DECIDUOUS BROADLEAF FORESTS BY *ACACIA* SPECIES

(1) Temperate deciduous broadleaf forests and their streams

In the northern hemisphere, typical dominant trees in temperate deciduous broadleaf forests (‘deciduous forests’ hereafter) include species of, e.g. *Quercus*, *Acer*, *Fagus*, *Betula*, *Ulmus* and *Tilia*. In mainland Portugal, deciduous forests predominate in the central and northern regions and are typically composed of a species mixture, with major contributors being *Quercus* spp., *Castanea*
sativa, Prunus spp. and Ulmus spp., very often including evergreen elements (e.g. Ilex aquifolium, Arbutus unedo, Laurus nobilis, Viburnum tinus, Phyllirea spp.) (Costa et al., 1998). In riparian areas, common species include Alnus glutinosa, Salix spp., Populus spp., Fraxinus angustifolia and Frangula alnus (Table 4). Of these species, A. glutinosa is an actinorhizal species that establishes symbiosis with the N-fixing actinobacteria Frankia alni, thus acting as an N-fixing tree species (Table 4). The coexistence of several tree species ensures diversity and redundancy of functional traits (Table 4), a key feature to guarantee stream multifunctionality and resilience to environmental changes (Kominoski et al., 2013).

In deciduous forests, streams are shaded from mid-spring to mid-autumn (i.e. when the tree canopy is fully developed; Fig. 1), which limits in-stream primary production (Bott et al., 1985; Alberts, Beaulieu & Buffam, 2017). In-stream primary production is also limited during the rest of the year (i.e. from mid-autumn to mid-spring) due to low insolation and low water temperatures (Bott et al., 1985; Alberts et al., 2017). Here, the riparian vegetation has a key functional role by fuelling streams with large amounts of plant litter, mostly senescent leaves, which constitute the primary source of carbon and energy for aquatic food webs (Abelho, 2001). Forest streams are, thus, heterotrophic systems (Bott et al., 1985; Hagen et al., 2010; Alberts et al., 2017). Litter inputs to streams occur mostly during autumn/winter when deciduous tree species shed their leaves (Abelho & Graça, 1996; Molinero & Pozo, 2004; Swan & Palmer, 2004). Differences in litter fall phenology and in litter decomposability among tree species allow the presence of organic matter in stream beds from autumn, when insect larvae start to hatch from eggs laid in summer, until spring, when water temperatures start to rise and insect larvae are ready to leave the aquatic environment and become winged adults (Molinero & Pozo, 2004). Streams and riparian forests are, thus, tightly linked by double transfer of energy and matter (e.g. plant litter flows from the vegetation to the streams, while adult invertebrates flow in the opposite direction) (Marks, 2019; Tolkkinen et al., 2020). Therefore, streams are highly sensitive to forest changes, including changes in tree species composition (Chauvet et al., 2016; Ferreira et al., 2016a).
**Invasive behaviour of *Acacia* species**

The *Acacia* genus (*Acacia* s.s. – formerly subgenus *Phyllodineae*; Leguminosae: Mimosoideae) is native to Australia, where it is the most diverse plant genus (Thiele *et al.*, 2011). Outside their native range, *Acacia* species frequently become invasive, with 24 species classified as such (Lorenzo, González & Reigosa, 2010; Richardson *et al.*, 2011; Lorenzo & Rodríguez-Echeverría, 2015). Additionally, many *Acacia* species are naturalized in their new locations and have the potential to become invasive (Castro-Díez *et al.*, 2011; Richardson *et al.*, 2011). In fact, *Acacia* is the tree genus with the most invasive species worldwide (Richardson *et al.*, 2011; Richardson & Rejmánek, 2011). Given that one-third of the world’s land surface has bioclimatic conditions similar to those present in the native range of *Acacia* species, the surface area they are likely to cover is expected to continue increasing (Richardson *et al.*, 2011).

The spread of *Acacia* species worldwide has been promoted mostly for the establishment of plantations for pulpwood, fuelwood and tannin production, which presently cover >3 million ha, but also for floriculture, especially in Europe (Griffin *et al.*, 2011). *Acacia* plantations worldwide will continue to be promoted to face growing demands by the paper industry (pulpwood) and by the rural population in less-developed countries where wood is still the primary source of energy (Griffin *et al.*, 2011; Kull *et al.*, 2011). It is thus expected that *Acacia* species will continue to escape human control and invade new areas.

*Acacia* species establish symbiotic relationships with root-nodule N-fixing bacteria (*Rhizobia* spp.) (Brockwell *et al.*, 2005), which affects soil characteristics and edaphic communities (Marchante *et al.*, 2008; Lorenzo *et al.*, 2010; Hellmann *et al.*, 2011; González-Muñoz, Costa-Tenorio & Espigares, 2012; Lazzaro *et al.*, 2014; Souza-Alonso, Novoa & González, 2014b), and facilitates *Acacia* species colonization of nutrient-poor soils (Table 5). The large number of invasive *Acacia* species and their wide ecological range enable them to establish in different habitats, including riparian areas (Table 5). Invasive *Acacia* species worldwide, e.g. *A. dealbata*, *A.
melanoxylon, Acacia longifolia, Acacia mangium and Acacia saligna, are mainly fast-growing species that out-compete native species (Le Maitre et al., 2011; Richardson, Roux & Wilson, 2015; Table 5). As the invasion progresses, Acacia cover and dominance increase, leading to a decrease in the richness and diversity of the native vegetation (Holmes & Cowling, 1997; Marchante, Marchante & Freitas, 2003; Fuentes-Ramírez et al., 2010; Hellmann et al., 2011; Le Maitre et al., 2011; González-Muñoz et al., 2012; Lorenzo et al., 2012; Marchante et al., 2015) and of other trophic levels (e.g. galler, their parasitoids and inquiline species; López-Núñez et al., 2017). Additionally, some species (e.g. A. dealbata, A. melanoxylon and A. mearnsii) can resprout and coppice with great vigour after cutting or a fire, re-invading the cleared areas very rapidly (Lorenzo et al., 2010; Vazquez-de-la-Cueva, 2014). Moreover, Acacia species produce numerous seeds that are viable for long periods and accumulate in long-lasting soil seedbanks (Richardson & Kluge, 2008; Gibson et al., 2011), which germinate after fire or clearing associated with control activities or other disturbance events. Several Acacia species produce allelopathic compounds, which may inhibit the germination of seeds or growth of other species (Souto et al., 2001; Lorenzo et al., 2010, 2011), although the role of allelopathy in the process of invasion has been considered mostly negligible under field conditions (Souza-Alonso et al., 2017). These characteristics allow Acacia species to be successful invaders in many areas, including riparian areas, forming (nearly) monospecific stands, altering the landscape and ecosystem services (Table 5; Fig. 2).

(3) Streams as invasion corridors

The spread of invasive plant species is often promoted by corridors, which are more effective if their spatial structure is based on a dense and connected network, such as streams and roads (Procheş et al., 2005; Christen & Matlack, 2006). Thus, connectivity in the landscape is a major driver of invasion (Procheş et al., 2005), with dispersal corridors promoting and determining the path of invasion (Wang et al., 2011; Vicente et al., 2014). Natural disturbance events associated with floods may also contribute to the role of streams as dispersal corridors (Tickner et al., 2001;
The role of such corridors is clear at the landscape scale when individuals of invasive species are found in large numbers near streams, but their numbers decrease as the distance from the initial propagule sources increases (Wang et al., 2011; Figueiredo, 2016; Oliveira-Costa et al., 2016).

Although Acacia species are primarily dispersed by ants or birds, depending on the dispersal system of each species, they may also be dispersed by water, especially when seeds are still inside the pods, with dispersal of, for example A. dealbata and A. mearnsii, being associated with watercourses in Portugal, Chile, and South Africa [Gibson et al. (2011) and references therein]. Seed dispersal by water (hydrochory) is an important dispersal mechanism for invasive riparian species, with seeds travelling long distances, while their germination rates are not affected by, or may even increase in, water (Kaproth & McGraw, 2008; Säumel & Kowarik, 2010; Rouifed et al., 2011; Schiedel & Tackenberg, 2013).

(4) Invasion of temperate deciduous broadleaf forests by Acacia species in Portugal

Acacia species were introduced into southern Europe (Portugal, Spain, France and Italy) by the 19th century for multiple purposes, namely as ornamental plants, to promote dune stabilization in coastal areas, to reduce erosion in mountainous areas, to increase soil fertility, and to supply tannin-rich bark for the tannery industry, and wood for cooperage and carpentry, and firewood (Fernandes, 2012, 2018). In some cases, Acacia species were planted by public services, illustrating their initial positive public perception (Carruthers et al., 2011). For instance, in Portugal between the end of the 19th century and early/mid-20th century, dune stabilization in coastal areas with A. longifolia, A. melanoxylon and A. saligna was carried out by the Portuguese forest agency, and afforestation of mountain areas with A. melanoxylon, A. dealbata and, to a lesser extent, five other Acacia species, was carried out under strategic plans to increase forest area or to reduce soil erosion (Fernandes, 2008, 2012, 2018). In France, Acacia species were used also as a source of aromatic essences for the perfumery industry, as cut flowers for floristry, and viewed from a tourism perspective.
perspective during the flowering period, economic activities that are still ongoing (Griffin et al., 2011; Kull et al., 2011).

The invasive potential of *Acacia* species in Portugal was recognized already in the 19th century (Fernandes, 2018). However, they only became a serious problem with the abandonment of rural areas, as a consequence of decreased interest in livestock production and agricultural activities, which left the land unmanaged and vulnerable to invasion. Additionally, the decline in the tannery industry and in the needs for charcoal left the established *Acacia* stands unmanaged, which facilitated *Acacia* species dispersal and invasion. Some *Acacia* species, namely *A. dealbata*, *A. melanoxylon* and *A. longifolia*, are among the most widespread invasive alien species in southern Europe (Lorenzo et al., 2010). In Portugal, *A. dealbata* and *A. melanoxylon* have become widespread invasive species in deciduous forests (Fig. 2), while *A. longifolia* is an aggressive invader of coastal dune systems (Kull et al., 2011). Several other species are clearly invasive, with the entire *Acacia* genus being listed as invasive by the Portuguese legislation, which forbids its further introduction and afforestation (Decree-Law no. 92/2019; Presidência do Conselho de Ministros, 2019).

In Portugal, the area dominated by *Acacia* species (e.g. *A. dealbata*, *A. melanoxylon* and *A. longifolia*) was already ~ 2,500 ha in 1977, mostly in the central and northern regions of the country, with another 95,100 ha showing scattered *Acacia* trees (Fernandes, Devy-Vareta & Rangan, 2013). In 2015, the area dominated by *Acacia* species was ~ 17,000 ha, with an increase of ~ 500 ha/year between 2005 and 2015 (ICNF, 2019). These figures are certainly underestimates because *Acacia* trees often co-occur with other species and in areas not classified as forest. The increase in *Acacia* cover over time is especially high in central and northern coastal areas, where the high level of disturbance of deciduous forests, promoted by different drivers (e.g. grazing, forest fires, agriculture and forestry), increased their susceptibility to invasion (Pereira & Figueiredo, 2015). The increase in *Acacia* cover is notorious at the landscape level, both for small and medium-sized watersheds. This is the case for the Arouce River watershed (central Portugal, 73 km²), where
the area covered by *A. dealbata* and *A. melanoxylon* has increased from 0.7% (1965) to 12.8% (2011) (Oliveira-Costa *et al*., 2016), an expansion that is considered one of the main landscape changes in this territory (Ornelas *et al*., 2018). The increase in *Acacia* cover is also significant in larger areas, such as the Ceira River watershed (central Portugal, 714 km²), where the area with a significant presence of *Acacia* species increased significantly between 1977 and 2018 (Fig. 3).

*Acacia* species are generally (in 97% of cases) associated with degraded habitats (ICNF, 2019). As the germination of *Acacia* species seeds is promoted by fire (Richardson & Kluge, 2008; Le Maitre *et al*., 2011), the severe rural fires that affected central Portugal in 2017 (San-Miguel-Ayanz *et al*., 2018; Fig. 3) will likely promote an increase in the area covered by these invasive species. In fact, the predicted increase in fire weather danger in Europe under climate change scenarios (i.e. increase in extreme fires that destroy large areas; San-Miguel-Ayanz *et al*., 2018) may be an important driver of large-scale *Acacia* invasion. Also, habitat fragmentation, by expanding the edge effect in the landscape, promotes the establishment of pioneer and fast-growing species, which frequently are invasive species (With, 2004).

The effects of invasion by *Acacia* species on terrestrial ecosystems have been frequently addressed (~ 500 papers published in the last 25 years) and reviewed (Le Maitre *et al*., 2011; Lorenzo & Rodríguez-Echeverría, 2015; Souza-Alonso *et al*., 2017), but studies addressing the effects of *Acacia* invasions on stream communities and functioning are scarce. We could identify only three studies to date (Lowe *et al*., 2008; Railoun, 2018; Wiener *et al*., 2020), despite several *Acacia* species being recognized as invasive in riparian habitats (Le Maitre *et al*., 2011; Richardson & Rejmánek, 2011; Lorenzo & Rodríguez-Echeverría, 2015). Based on the assumption that it is possible to anticipate the effects of *Acacia* invasion on stream ecosystems by considering the characteristics of deciduous forest trees and of *Acacia* species (*A. dealbata* and *A. melanoxylon*), we propose a conceptual model to predict the effects of *Acacia* invasion on stream water quality and quantity, litter inputs to streams, aquatic communities and litter decomposition.
IV. ANTICIPATED EFFECTS OF ACACIA INVASION OF RIPARIAN AREAS ON STREAMS – A CONCEPTUAL MODEL

(1) Changes in water quality

Soils in Acacia stands generally have higher N concentrations than soils with lower densities of N-fixing species, as a result of N-rich root exudates from Acacia trees and decomposition of N-rich litter (Marchante et al., 2008; Lorenzo et al., 2010; Hellmann et al., 2011; González-Muñoz et al., 2012; Lazzaro et al., 2014; Souza-Alonso et al., 2014b). Litter from some Acacia species, especially those with phyllodes (i.e. leaf-like structures derived from modified petioles, ‘leaves’ hereafter; e.g. A. melanoxylon, A. longifolia and A. saligna) decompose slowly, accumulating in a thick layer on the soil surface, and promoting continuous N enrichment of the soil (Marchante et al., 2008, 2019; Incerti et al., 2018). The N-rich soil of Acacia stands changes the N nutrition of nearby non-N-fixing plants that are able to use fixed atmospheric N (Hoogmoed et al., 2014), which can translate into an increase in their foliar N concentration (Hellmann et al., 2011). Increases in foliar N concentration in non-N-fixing species growing in the presence of N-fixing species seem to be common. A meta-analysis found higher foliar N concentration in non-N-fixing species growing in mixed tree plantations with N-fixing species than in monocultures, while no change in foliar N concentration was found when the mixture did not include N-fixing species (Richards et al., 2010). Also, foliar N concentration was higher in non-N-fixing species when growing under than away from the canopy of N-fixing native Alnus crispa in different ecosystems in Alaska (Rhoades et al., 2001). N-rich soil leachates and in-stream decomposition of N-rich litter inputs from the riparian vegetation (both Acacia litter and litter from native species growing in Acacia stands) may contribute to increased N concentrations in streams flowing through Acacia stands, as occurs in streams flowing through stands dominated by other N-fixing woody species [native Alnus spp. (Compton et al., 2003; Shaftel, King & Back, 2012); invasive species (Goldstein et al., 2009; Atwood et al., 2010; Mineau et al., 2011; Wiegner et al., 2013; Stewart et al., 2019)] (Tables 1, 2; Fig. 4). However, the magnitude of increases in N concentrations in streams will likely depend on...
the stand density, extent and duration of the invasion as well as on the characteristics of the native and invasive species. For instance, N concentrations in stream water generally increase with increasing cover by N-fixing species at the watershed scale [Alnus spp. (Shaftel et al., 2012); E. umbellata (Goldstein et al., 2009); U. europaeus (Stewart et al., 2019)]. When N-fixing species are only in the riparian area, increases in cover affect stream water N concentrations much less or the effects are negligible [A. rubra (Compton et al., 2003; Kominoski et al., 2011)].

The effects of Acacia invasion on dissolved phosphorus (P) concentration are more difficult to anticipate. Increases in N availability in stream water could lead to decreases in P concentration due to increased P uptake by microbes. Indeed, a negative correlation between NO$_3$-N and dissolved reactive P was found for streams flowing through riparian areas invaded by the N-fixing U. europaeus (Stewart et al., 2019). However, other studies comparing streams flowing through areas invaded by N-fixing species and non-invaded areas found no significant differences in P concentrations in stream water (Atwood et al., 2010; Mineau et al., 2011; Wiegner et al., 2013).

(2) Changes in water quantity

Invasion of deciduous forests by Acacia species may decrease stream water availability because these fast-growing evergreen species establish very dense stands, which translates into high transpiration rates with consequent decreases in soil water content (Dye & Jarmain, 2004; Le Maitre et al., 2015; Lorenzo & Rodríguez-Echeverría, 2015) (Fig. 4). Water consumption by A. melanoxylon was estimated as being very high (higher than that of Eucalyptus globulus and Pinus pinaster, which are regarded as having high water demands) in a dense stand in the north-western Iberian Peninsula (Jiménez et al., 2010). In South Africa, water uptake by Acacia species (including A. dealbata and A. melanoxylon) accounted for a substantial portion of the mean annual runoff (Le Maitre, Versfeld & Chapman, 2000). Changes in water uptake and runoff are generally stronger when invasive and native species differ most in structure and deciduousness and where water availability is higher (Le Maitre et al., 2015; Mkunyana et al., 2019). Thus, potential strong effects
on stream water availability are expected when deciduous forests with seasonal dormancy are replaced by evergreen Acacia species, especially in riparian areas. The high water demand by Acacia species may result in flow intermittency during the warmest and driest periods of the year, which are expected to increase in frequency and duration under a global change scenario, particularly in Mediterranean areas (IPCC, 2013).

(3) Changes in litter inputs to streams

(a) Changes in the diversity of litter inputs

Invasive Acacia species have strategies to increase their cover and out-compete native species (Table 5), which frequently leads to the establishment of pure Acacia stands (Hellmann et al., 2011; Lorenzo et al., 2012; Marchante et al., 2015). As invasion proceeds, the contribution of Acacia species to litter inputs to streams will likely increase. At early stages of invasion this will translate into an increase in the diversity of litter inputs, since there will be a higher number of species in the riparian vegetation (Fig. 4). However, as invasion progresses and native species are replaced by Acacia species, the diversity of litter inputs may dramatically decrease and these may become dominated by Acacia litter (Fig. 4), which contrasts with litter inputs to streams flowing through more diverse deciduous forests (Lecerf et al., 2005; Swan, Gluth & Horne, 2009; Ferreira et al., 2016a).

(b) Changes in the phenology of litter inputs

Changes in the timing of litter inputs to streams are also expected with Acacia invasions (Fig. 4). While in deciduous forests trees shed their leaves mainly in autumn/winter (Abelho & Graça, 1996; Molinero & Pozo, 2004), in evergreen Acacia stands litter inputs are expected year-round, eventually with a summer peak due to water stress, as observed for other evergreens (e.g. Abelho & Graça, 1996; Molinero & Pozo, 2004) (Table 4). Acacia species also shed pods and seeds in summer (Lorenzo et al., 2010), which may contribute to the organic matter input peak in this season.
Moreover, the accumulation of large amounts of Acacia litter on soils as a result of slow decomposition, at least for species with phyllodes (Incerti et al., 2018; Marchante et al., 2019), may lead to high amounts of lateral litter inputs to streams during high rainfall events on steep slopes.

(c) Changes in the typology of litter inputs

Streams flowing through Acacia stands may also differ from those in native forests in the typology of litter inputs (Fig. 4). The contribution of reproductive structures (flowers and pods) and woody material (twigs) to litter fall in Acacia stands may be substantial (34–54% across several Acacia species; Milton, 1981) compared with litter fall in deciduous forests (Abelho & Graça, 1996; Molinero & Pozo, 2004). The input of large woody material (branches and logs) to streams may also be high in Acacia stands, especially in steep and stony mountain slopes dominated by A. dealbata (Fig. 5B) due to the short-lived condition of this species (A. dealbata longevity is 30–40 years; Table 4) and the collapse of trees associated with their shallow root system, a feature that contributes to their high susceptibility to landslides (Figueiredo, Pupo-Correia & Sequeira, 2013).

(d) Changes in the quantity of litter inputs

The above-mentioned changes in the diversity, phenology and typology of litter inputs will likely affect litter input dynamics to streams in Acacia stands (Railoun, 2018). Thus, it is possible that the annual amount of litter input to streams in Acacia stands will differ from that of streams in deciduous forests (Fig. 4); the magnitude and direction of the change is, however, difficult to anticipate as it depends on the magnitude of the above-mentioned changes, which in turn depend on the characteristics of deciduous forests and Acacia stands.

(e) Changes in the quality of litter inputs

Physical (e.g. toughness) and chemical (e.g. concentrations of nutrients and structural and secondary compounds) characteristics differ among leaf species and organic matter types (e.g.
leaves, flowers, fruits, wood) (Molinero & Pozo, 2006; Castro-Díez et al., 2012; Table 4). Thus, changes in diversity, typology and quantity of litter inputs to streams in Acacia stands will likely be accompanied by changes in nutrient inputs (Fig. 4). The direction and magnitude of these changes will also depend on the species composition of the invaded systems. If a deciduous forest dominated by species such as C. sativa and Quercus spp. is invaded by A. dealbata, there will likely be an increase in litter N inputs to streams, as the invasive species is richer in N than the natives (Castro-Díez et al., 2012). Changes are expected even when A. dealbata invades riparian areas dominated by native N-fixing species, such as Alnus glutinosa, resulting from differences in litter input phenology, typology and quantity.

(f) Changes in allelopathic compounds

Finally, Acacia species produce a large number of allelopathic compounds. Souza-Alonso, González & Cavaleiro (2014a) identified 74 volatile organic compounds (VOCs) produced by A. dealbata (in flowers, leaves and litter) and reported negative effects of VOCs on germination and early seedling growth of native plant species in laboratory trials. Probably VOCs are not a major concern after Acacia litter enters streams. However, Acacia species also produce a high number of non-volatile (water-soluble) chemical compounds (Aguilera et al., 2015), which may affect aquatic communities and litter decomposition. Leachates from green leaves and leaf, flower and pod litter from A. dealbata have the ability to inhibit germination and seedling and radicle growth of a model plant species (Lactuca sativa) in laboratory trials, with inhibition being stronger during Acacia species blossoming (Carballeira & Reigosa, 1999; Aguilera et al., 2015). Similar results were found using leachates of decomposing A. melanoxylon leaf litter, especially at early stages of decomposition (González, Souto & Reigosa, 1995). Additionally, leachates of A. dealbata change soil bacterial functional diversity and reduce bacterial richness and diversity in pine forests, but not in mixed oak forests (Lorenzo, Pereira & Rodríguez-Echeverría, 2013). Thus, it is reasonable to
assume that leachates released from *Acacia* litter after immersion in streams may inhibit litter colonization by microbes and litter decomposition (Fig. 4).

(4) Changes in stream litter decomposition and aquatic communities

(a) Response to changes in water quality

Litter decomposition is a fundamental process in forest streams, allowing the incorporation of litter carbon and nutrients into the aquatic food web thus promoting nutrient cycling (Wallace *et al.*, 1997; Marks, 2019). Litter decomposition is mostly a biological process, carried out by microbial decomposers, mainly aquatic hyphomycetes, and benthic invertebrates, mainly shredders (Gessner *et al.*, 2010; Marks, 2019), which are sensitive to environmental changes. Moderate increases in dissolved N availability stimulate microbial activity [e.g. reproduction, growth and metabolism (Gulis & Suberkropp, 2003; Gulis, Ferreira & Graça, 2006)], invertebrate colonization of litter [e.g. taxa richness, abundance and biomass (Gulis *et al.*, 2006; Greenwood *et al.*, 2007)] and consequently litter decomposition in streams (Woodward *et al.*, 2012; Ferreira *et al.*, 2015a; Rosemond *et al.*, 2015). Expected increases in dissolved N availability in streams flowing through *Acacia* stands may thus stimulate microbial activity, invertebrate colonization and ultimately litter decomposition (Fig. 4).

Effects of increases in N concentration in stream water may, however, depend on background N and P concentrations. When background N concentrations are not limiting, moderate increases in N concentrations may not have noticeable effects on aquatic communities or litter decomposition (Chadwick & Huryn, 2003; Baldy *et al.*, 2007). Thus, effects of nutrient enrichment tend to be lower when background nutrient concentrations are higher (Ferreira *et al.*, 2015a). Also, when background P concentrations are limiting, increases in N concentrations may not have noticeable effects on litter decomposition (Ferreira *et al.*, 2015a). Additionally, effects of N enrichment may be stronger for larger N increases (Ferreira *et al.*, 2015a), which may relate to the extent and duration of the invasion.
The impact of increases in stream water N availability on decomposer activity and litter decomposition may also depend on litter characteristics. Nutrient effects on microbial activity and litter decomposition are generally stronger for nutrient-poor than for nutrient-rich litter, where microbial activity is generally not nutrient limited (Gulis & Suberkropp, 2003; Ferreira, Gulis & Graça, 2006b; Gulis et al., 2006; Kominoski et al., 2015). Moreover, nutrient effects are generally stronger for lignin-poor than for lignin-rich litter, where microbial activity may be carbon (C) limited since lignin is highly refractory and also limits microbial access to labile C sources (Jabiol et al., 2019).

Therefore, changes in microbial activity and litter decomposition in streams in Acacia stands will finally depend on the interaction between increases in dissolved N availability and litter characteristics. Acacia leaves are N-rich, but N accessibility to microbes may depend on leaf toughness and lignin concentration. For instance, A. melanoxylon leaf litter is tough and has high lignin concentration (low C quality). Consequently, litter decomposition is slow and may be less sensitive to dissolved nutrient concentration than that of litter with higher C quality (Ferreira et al., 2016b).

Woody materials are abundant in Acacia-dominated streams (Fig. 5B). They have high C to N ratios and are sensitive to increases in dissolved nutrient concentrations (Gulis et al., 2004; Gulis, Suberkropp & Rosemond, 2008; Ferreira et al., 2006b). Recalcitrant litter (e.g. tough leaves and woody material) is, however, colonized slowly, sustains lower microbial activity and is decomposed at a lower rate than high-quality litter (i.e. soft, with high nutrient concentrations and low concentrations of secondary and structural compounds) (Ferreira et al., 2006b; Gulis et al., 2008).

Thus, despite possible stimulation of litter decomposition by increases in dissolved N availability in streams flowing through Acacia stands, if these streams receive higher proportions of recalcitrant litter compared with streams in deciduous forests, the absolute rate of litter decomposition may still be lower in the invaded than in the native streams. A reduction in overall litter decomposition may impair nutrient cycling through the food web (Hladyz et al., 2011).
Additionally, the impact of nutrient enrichment on litter decomposition may depend on the presence of shredders. Feeding activities of shredders on leaves are stimulated by litter microbial conditioning (Bärlocher & Sridhar, 2014), which is promoted by increases in water nutrient concentration (Gulis & Suberkropp, 2003; Gulis et al., 2006). Thus, when shredders are present, they may amplify the stimulatory effect that nutrient enrichment has on microbial communities (Gulis et al., 2006). On the contrary, if shredder abundance decreases in streams in Acacia stands as a result of stream flow intermittency or litter recalcitrance (see Section IV.4b, IV.4c), effects of nutrient enrichment on litter decomposition may be limited.

(b) Response to changes in water quantity

Decreases in water quantity in streams in Acacia stands may also impair aquatic communities and processes (Fig. 4). Benthic macroinvertebrate biodiversity and abundance are lower in intermittent than in permanent streams (Datry et al., 2011; Soria et al., 2017). Microbial and invertebrate activity on leaf litter is inhibited when litter is emersed (e.g. dry stream bed, as in intermittent streams) than immersed in stream water (e.g. permanent streams or permanent sections of intermittent streams) (Richardson, 1990; Corti et al., 2011; Foulquier et al., 2015; Abril, Muñoz & Menéndez, 2016). Even when leaf litter is emersed only during the early phases of litter decomposition (i.e. the stream bed is still dry when litter falls in), microbial and invertebrate colonization of and activity on leaf litter are generally impaired, which in turn may lead to slower litter decomposition (Maamri et al., 2001; Monroy et al., 2016). The effects of flow intermittency on aquatic invertebrate communities may be long lasting and lead to decreases in litter decomposition even after flows resume (Datry et al., 2011).

(c) Response to changes in litter input characteristics

Increases in Acacia species cover and changes in litter input characteristics may also affect aquatic communities, especially those involved in the detrital pathway, which strongly depend on
litter inputs for food and substrate (Wallace et al., 1997; Gessner et al., 2010) (Fig. 4). Species richness of aquatic hyphomycetes and benthic macroinvertebrates is generally positively correlated with species richness of riparian trees and benthic litter (Laitung & Chauvet, 2005; Lecerf et al., 2005; Ferreira et al., 2016a). A decrease in riparian tree diversity in Acacia stands may thus lead to decreases in aquatic biological diversity and abundance, as shown for the replacement of deciduous forests by E. globulus monocultures (Bärlocher & Graça, 2002; Ferreira et al., 2006a, 2015b; Larrañaga, Basaguren & Pozo, 2009). Lowe et al. (2008) also found lower abundances of cobble-dwelling taxa and higher abundances of particle-feeding mayflies and chironomids in streams flowing through areas invaded by A. mearnsii than in streams flowing through native Fynbos vegetation in South Africa. Decreases in the diversity, abundance and biomass of macroinvertebrates (shredders in particular) generally lead to decreases in litter decomposition (Piscart et al., 2009; Ferreira et al., 2016a; Monroy et al., 2016).

However, aquatic hyphomycete communities are generally functionally redundant in the sense that different communities are able to carry out litter decomposition at similar rates when a common litter species is considered (e.g. Bärlocher & Graça, 2002; Ferreira et al., 2006a). Nevertheless, as litter quality is expected to change in streams in Acacia stands, it is also expected that microbially driven litter decomposition may differ between Acacia-dominated and native streams. Acacia dealbata leaf litter may impose an additional challenge to aquatic communities as the small leaflets can detach easily after immersion and be carried downstream by water currents before they enter the local aquatic food web.

Changes in litter decomposition rates in streams in Acacia stands, and consequently in nutrient cycling, are therefore difficult to anticipate since they depend primarily on how stream water quality and quantity, litter inputs and aquatic communities will change in response to the Acacia invasion of deciduous forests. However, if the changes discussed above are confirmed (Fig. 4), Acacia species may well act as transformers (ecosystem engineers) of aquatic ecosystems as they do for terrestrial ecosystems (Richardson & Rejmánek, 2011).
Effects of Acacia invasions on soil detrital pathways have been documented (Ehrenfeld, 2003; Souza-Alonso et al., 2017). For instance, the invasion of South African grasslands by A. dealbata led to decreases in dung coleopteran species richness, abundance and body size, with consequent changes in community composition (Coetze, Rensburg & Robertson, 2007). Invasion by A. melanoxylon and A. mearnsii in South Africa led to decreases in soil invertebrate species richness, but not family richness, suggesting that changes in species richness may not be translated into functional changes (Samways, Caldwell & Osborn, 1996). The effects of Acacia invasion on soil invertebrates may be mediated by detrimental effects on species ecology. Sousa et al. (1998) found lower growth rates and growth efficiencies of the isopod Porcellio dilatatus when fed with A. longifolia than with native Alnus glutinosa or Quercus sp. leaves, despite the higher consumption of A. longifolia litter (likely due to compensatory feeding).

V. CONCEPTUAL FRAMEWORK TO PREDICT EFFECTS OF INVASION OF RIPARIAN AREAS BY N-FIXING SPECIES ON STREAMS

Effects induced by the invasion of temperate deciduous broadleaf forests by N-fixing species (e.g. Acacia spp.) predicted by our conceptual model (Fig. 4) can be illustrated considering a continuum from early to advanced stages of invasion of riparian forests with (i) low and (ii) high representation of N-fixing species (Fig. 6). Riparian forests with low representation of N-fixing species are dominated by early colonizer species, such as Salix spp., and have low riparian tree species richness and cover by N-fixing species, such as Alnus glutinosa (Fig. 6A, B). On the other hand, forests with high representation of N-fixing species are dominated by A. glutinosa, which is a consolidator species typical of mature riparian forests, and have higher riparian tree species richness and cover by N-fixing species (Fig. 6A, B). Cover by N-fixing species affects water N concentration, which is lower in streams flowing through forests with low than high representation of N-fixing species (Compton et al., 2003; Goldstein et al., 2009; Kominoski et al., 2011; Shaftel et al., 2012; Stewart et al., 2019; Fig. 6C). Given the high evapotranspiration of Salix atrocinerea...
(assuming strong similarities with *Salix cinerea*) compared to *A. glutinosa* (Kučerová *et al.*, 2001).

discharge is expected to be lower in streams flowing through forests with low than high
representation of N-fixing species (Fig. 6D). Owing to the lower water N concentration and lower
nutritional quality of the litter input (e.g. lower litter N concentration) in streams flowing through
forests with low cover of N-fixing species, litter decomposition potential (i.e. overall decomposition
of benthic organic matter) is expected to be lower in these streams compared with streams flowing
through forests dominated by N-fixing species that have higher water N concentration and receive
soft, N-rich *A. glutinosa* litter (Fig. 6E, F).

During invasion by *Acacia* species, riparian tree species richness first increases, while at
advanced stages of invasion it decreases as the riparian vegetation becomes a (nearly) monospecific
*Acacia* stand (Section III.2; Table 5; Fig. 6A). During invasion, cover by N-fixing species also
increases as the cover by *Acacia* species increases (Fig. 6B). Consequently, water N concentration
increases (Fig. 6C) through the pathways described above (Section IV.1; Fig. 4). Stream discharge
decreases (Fig. 6D) as the evergreen, fast-growing *Acacia* form dense stands, translating into
increased evapotranspiration (Section IV.2; Fig. 4). Litter decomposition potential increases with
increases in water N concentration and litter input diversity at early stages of invasion (Fig. 6E, 6F),
as decomposer activity is promoted by increased nutrient availability (‘productivity hypothesis’)
and substrate diversity (‘niche complementarity hypothesis’) (Ferreira *et al.*, 2016a; Sections IV.4a,
IV.4c; Fig. 4). At advanced stages of invasion, litter decomposition potential can increase further
(Fig. 6E), if effects mediated by increased water N concentrations prevail (Section IV.4a; Fig. 4), or
it can decrease (Fig. 6F), if effects mediated by increases in litter recalcitrance (e.g. increases in
wood inputs) prevail when the riparian vegetation is dominated by *Acacia* (Section IV.4a; Fig. 4).

When invasion promotes streambed drying, litter decomposition can be further reduced (Section
IV.4b). The effects of invasion on stream processes will depend on the interactions of multiple
pathways and are therefore more difficult to predict compared with changes in environmental
variables. At early stages of *Acacia* invasion, effects are small and differences between forests with
low and high representation of N-fixing species are maintained compared with the pre-invasion condition. At advanced stages of invasion, however, effects become stronger and similar for both forest types as the riparian vegetation becomes a monospecific Acacia stand (Fig. 6). Although the final effects of Acacia invasion may be similar for riparian forests with low or high representation of N-fixing species, the magnitude of the effects will differ given the initial differences between forest types (Fig. 6).

VI. DECOMPOSITION OF ACACIA LEAF LITTER IN STREAMS

To understand fully the effects of Acacia invasion of riparian areas on stream communities and processes we need to consider the multiple pathways described above (Fig. 4). However, comparisons of non-invaded and invaded conditions (either spatially different conditions, e.g. non-invaded versus invaded streams, or temporally different conditions, e.g. the same stream before and during invasion) are scarce (Table 1). Nevertheless, studies addressing litter decomposition in streams have used leaf litter of different Acacia species, both with phyllodes and ‘true’ leaves, and they can inform its decomposition potential.

Reported decomposition rates ($k$, day$^{-1}$) for Acacia leaf litter vary from slow ($k < 0.005$) to medium ($0.005 < k < 0.010$) to fast ($k > 0.010$) [using Petersen & Cummins (1974) categories of decomposition rates], both within and across species (Table 6). However, comparisons among species, or even within species, are limited by differences in the type of Acacia leaves, methodologies, and incubation conditions. Still, it seems that litter decomposition (at least for A. longifolia and A. melanoxylon, which have phyllodes) is mostly microbial-driven (Table 6). Also, litter decomposition rates are sensitive to environmental conditions (e.g. Campbell et al., 1992; Serra & Abelho, 2018; Table 6). The only study that compared Acacia (A. mearnsii, with ‘true’ leaves) litter decomposition in streams flowing through Acacia stands and native vegetation (Fynbos) found no significant differences between stream types, although decomposition was faster for A. mearnsii than for Fynbos species (Railoun, 2018). These latter results contrast with our
proposed model (Figs 4, 6), but we need to bear in mind that Fynbos vegetation is dominated by evergreen sclerophyllous plants, which likely produce recalcitrant litter that decomposes more slowly than that of *A. mearnsii*. This highlights the need to consider differences in the invaded/invasive system when comparing results across studies and extrapolating the conceptual model to other systems.

**VII. IMPACTS OF INVASIVE N-FIXING SPECIES ON ECOSYSTEM SERVICES PROVIDED BY STREAMS**

The effects of alien tree species on services provided by terrestrial ecosystems vary with the (type of) ecosystem service, biome, type of native ecosystem, and functional group of the alien species, among other factors (Castro-Díez et al., 2019). Similar information is lacking for their effects on services provided by stream ecosystems. The replacement of diverse forests by monospecific stands reduces functional diversity and redundancy, jeopardizing key stream processes and, consequently, the services they provide to humans (Table 7). Affected stream ecosystem services may include: provisioning services such as the supply of good-quality water; regulating services such as litter decomposition and nutrient cycling; supporting services such as biodiversity; and cultural and life-enhancing services such as recreation (Le Maitre *et al.*, 2011; Table 7).

Many stream processes are important not only locally but also downstream; for instance, litter decomposition releases dissolved nutrients and fine particulate organic matter that can be incorporated into food webs downstream (MacDonald & Coe, 2007; Wipfli, Richardson & Naiman, 2007). Additionally, stream processes are important to the riparian ecosystem; for instance, aerial stages of aquatic insects can be food for riparian predators (Nakano & Murakami, 2001; Chika, Iwata & Eitaro, 2004; Baxter, Fausch & Saunders, 2005). Thus, local changes to stream ecosystem functioning may have far-reaching consequences. The potential for strong effects of invasive N-
fixing species on stream functioning, and consequently on ecosystem services, make management of invasions in riparian forests a priority.

VIII. FUTURE DIRECTIONS

The proposed conceptual model provides guidelines for research on the effects of invasion of riparian forests by alien N-fixing species. For the large majority of invasive N-fixing species, the pathways, magnitude and direction of effects still need to be clarified. To understand fully the effects of species invasions on stream ecosystems, streams flowing through invaded and non-invaded riparian forests need to be compared. A before–after approach, which compares streams before and after invasion, may be used when historical information (i.e. prior to invasion) exists. A before–after control-impact (BACI) approach can be used to correct observations for temporal changes in other environmental factors (e.g. ambient temperature, atmospheric N deposition). In this case, the before–after condition is compared for two sets of streams: streams that underwent invasion and streams that did not undergo invasion and still flow through native forests (Mineau et al., 2012).

However, historical data may not be available. In this case, comparisons may need to be limited to streams flowing through native forests and streams flowing through invaded areas (Wiegner et al., 2013; Railoun, 2018). If an invasion gradient is available (i.e. with increasing cover of the invasive species) we may use a space-for-time approach (Goldstein et al., 2009; Stewart et al., 2019), and investigate invasion thresholds (i.e. minimum cover of the invasive species for which effects are measurable), which can help prioritize recovery interventions. In any case, as the magnitude and direction of the effects of species invasion on streams depend on background conditions (e.g. characteristics of the native vegetation, water quality), extrapolation of effects to different environmental conditions should be done with caution.

Effects of invasions should be assessed on multiple stream components (i.e. sediments, water, organic matter, communities and processes) and ideally include the stream–riparian forest meta-
ecosystem. Importantly, effects of invasion by N-fixing species on the multiple components of stream ecosystems need serious attention as these may influence multiple ecosystem services (Table 7). Determining the pathways of action (e.g. via changes in water quality, water quantity, quantity and quality of litter inputs) will be useful for the establishment of mitigation measures.

IX. CONCLUSIONS

(1) Forest invasion by alien tree species may have cross-ecosystem effects. Forest streams largely depend on riparian vegetation as a source of carbon, nutrients and energy, and are sensitive to changes in forest composition. Effects of tree invasion on streams may be especially strong when alien and native species differ most in their traits, as when native deciduous forests with low representation of N-fixing species are invaded by fast growing, evergreen N-fixing species. The magnitude of the effects will also depend on the extent and duration of the invasion.

(2) Invasion of deciduous forests by Acacia species may affect stream ecosystems via multiple pathways: changes in water quality (e.g. increases in N concentration), changes in water quantity (e.g. decreases in water availability) and changes in litter input characteristics (e.g. decreases in litter diversity, changes in quantity, quality and timing). Consequently, aquatic communities and processes may be affected.

(3) The magnitude and direction of the effects of tree invasion on aquatic communities and processes will nevertheless depend on interactions among the multiple pathways that may have opposite effects, e.g. increases in N concentration may stimulate litter decomposition while decreases in water availability may inhibit it.

(4) The multiple effects of tree invasion on streams may jeopardize the services that these ecosystems provide to human populations, which is of great concern given the small area occupied by streams worldwide and the strong dependency of humans on their services (e.g. good quality water).
(5) Given the potential effects of N-fixing tree invasion on stream ecosystem services, it is surprising how little research there is on this topic compared with that addressing the effects of other environmental changes. The proposed model helps to anticipate effects of forest invasion by N-fixing trees on streams, but the magnitude of these effects still remains to be quantified. Research on the effects of forest invasion on streams should be a priority as is the case for other human-induced environmental changes (e.g. emerging contaminants), allowing better management of stream–riparian forest meta-ecosystems.

X. ACKNOWLEDGEMENTS

Comments by two anonymous reviewers on an early version of this review were greatly appreciated. This study was financed by the Portuguese Foundation for Science and Technology (FCT), through the strategic projects UIDP/04292/2020 granted to MARE – Marine and Environmental Sciences Centre and UIDB/04004/2020 granted to CFE – Centre for Functional Ecology. Financial support granted by the FCT to V.F. (IF/00129/2014, CEECIND/02484/2018) and A.P. (SFRH/BD/118069/2016) is also acknowledged.

XI. REFERENCES


AGUILERA, N., BECERRA, J., VILLASEÑOR-PARADA, C., LORENZO, P., GONZÁLEZ, L. & HERNÁNDEZ,


Celesti-Grapow et al. (2009).


EFlora.org (2015). Taiwan Invasive Species Database.


instrumentos de gestão territorial. O caso paradigmático do género *Acacia* em Portugal.


GESSERT, M. O., SWAN, C. M., DANG, C. K., MCKIE, B. G., BARDGETT, R. D., WALL, D. H.


associated fungi and invertebrates by moderate eutrophication: implications for stream 

nutrient enrichment on the decomposition of wood and associated microbial activity in 
streams. *Freshwater Biology* 49, 1437–1447.

GULIS, V. & SUBERKROPP, K. (2003). Leaf litter decomposition and microbial activity in nutrient-

and leaf litter in unaltered and nutrient-enriched headwater streams. *Applied and 
Environmental Microbiology* 74, 1094–1101.

invasion of the exotic tree *Ailanthus altissima* affect the soil arthropod community? The case 
48.

allochthonous input and autochthonous production in streams along an agricultural land-use 

*Freshwater Science* 32, 343–358.

Impact of an exotic N₂-fixing *Acacia* on composition and N status of a native Mediterranean 
community. *Acta Oecologica* 37, 43–50.


spatio-temporal rates, patterns and determinants of biological invasions in forest ecosystems. 


Adoption, use and perception of Australian acacias around the world. *Diversity and Distributions* 17, 822–836.


Le Maître, D. C., Versfeld, D. & Chapman, R. (2000). The impact of invading alien plants on...


Lisboa.


of Stellenbosch.


RICHARDSON, D. M., HOLMES, P. M., ESSLER, K. J., GALATOWITSCH, S. M., STROMBERG, J. C.,


Here to stay. Recent advances and perspectives about *Acacia* invasion in Mediterranean areas. *Annals of Forest Science* **74**, 55.


Table 1. Effects of the invasion of riparian areas by alien N-fixing woody species, assessed by comparisons between streams in non-invaded areas and streams with the riparian area invaded by N-fixing species, as reported in the literature.

<table>
<thead>
<tr>
<th>Invasive species</th>
<th>Native region</th>
<th>Study region and native vegetation</th>
<th>Stream characteristic</th>
<th>Effects of the invasion (response in invaded compared with non-invaded condition)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acacia mearnsii</em> (black wattle)</td>
<td>Australia</td>
<td>Cape Floristic Region, South Africa; Fynbos shrubland</td>
<td>Benthic macroinvertebrates</td>
<td>Lower abundance of cobble-dwelling taxa; higher abundance of particle-feeding mayflies and chironomids</td>
<td>Lowe <em>et al.</em> (2008)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Litter fall dynamics (~ litter input dynamics)</td>
<td>Higher annual amount of litter fall; change in phenology of litter fall; higher N concentration in leaf litter</td>
<td>Railoun (2018)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Decomposition of native and <em>A. mearnsii</em> leaf litter in fine mesh bags</td>
<td>No effect of invasion; faster decomposition of <em>A. mearnsii</em> than native litter</td>
<td>Railoun (2018)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Macroinvertebrate density associated with native and <em>A. mearnsii</em> leaf litter decomposing in coarse mesh bags</td>
<td>No effect of invasion or litter type</td>
<td>Railoun (2018)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Sediment-associated nutrients</td>
<td>Higher total C and total P concentrations in sediments (but context dependent)</td>
<td>Wiener <em>et al.</em> (2020)</td>
</tr>
<tr>
<td><em>Elaeagnus angustifolia</em> (Russian olive)</td>
<td>Western and Central Asia</td>
<td>Western USA; sagebrush steppe</td>
<td>Stream water quality</td>
<td>Higher organic N concentration</td>
<td>Mineau <em>et al.</em> (2011)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Nutrient limitation of biofilms</td>
<td>Lower N limitation</td>
<td>Mineau <em>et al.</em> (2011)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Ammonium (NH$_4$-N), nitrate (NO$_3$-N) and phosphate (PO$_4$-P) uptake</td>
<td>Higher demand for NH$_4$-H and NO$_3$-N at inorganic N low background concentrations</td>
<td>Mineau <em>et al.</em> (2011)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Litter fall (~ litter input)</td>
<td>Higher amount of litter fall</td>
<td>Mineau <em>et al.</em> (2012)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Leaf litter decomposition</td>
<td>No effect of invasion; faster decomposition of <em>E. angustifolia</em> than native <em>Salix amygdaloides</em> litter</td>
<td>Mineau <em>et al.</em> (2012)</td>
</tr>
<tr>
<td>Species</td>
<td>Geographical Location</td>
<td>Environmental Impact</td>
<td>Reference</td>
<td></td>
<td></td>
</tr>
<tr>
<td>-------------------------</td>
<td>-----------------------</td>
<td>---------------------------------------</td>
<td>------------------------------</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Instream primary production</td>
<td>No change despite reduction in canopy cover</td>
<td>Mineau et al. (2012)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Benthic organic matter</td>
<td>Higher storage; no changes in ecosystem respiration; no change in organic matter export</td>
<td>Mineau et al. (2012)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stream ecosystem efficiency</td>
<td>Lower respiration/organic matter input ratio</td>
<td>Mineau et al. (2012)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Elaeagnus umbellata</strong> (autumn-olive)</td>
<td>Eastern Asia; Eastern USA; deciduous broadleaf forest</td>
<td>Positive correlation between NO$_3$-N and <em>E. umbellata</em> cover</td>
<td>Goldstein et al. (2009)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Falcataria moluccana</strong> (albizia)</td>
<td>Maluku Islands, New Guinea Island, Bismarck Archipelago and Solomon Islands</td>
<td>Higher NO$_3$+NO$_2$ concentration</td>
<td>Atwood et al. (2010)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Food-web structure</td>
<td><em>F. moluccana</em> became a major contributor to diets of lower-level consumers, displacing particulate organic matter and macroalgae; <em>F. moluccana</em> likely is an important N source for benthic primary producers</td>
<td>Atwood et al. (2010)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stream water quality</td>
<td>Higher NO$_3$+NO$_2$ concentration; lower organic N and organic C concentrations</td>
<td>Wiegner et al. (2013)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nutrient limitation of biofilms</td>
<td>Higher benthic chlorophyll-α; lower N limitation</td>
<td>Wiegner et al. (2013)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Ulex europaeus</strong> (European gorse)</td>
<td>British Isles and Western Europe; Banks Peninsula, New Zealand; podocarp forest</td>
<td>Higher NO$_3$ concentration due to decomposition of <em>U. europaeus</em> litter; positive correlation between NO$_3$ concentration and <em>U. europaeus</em> cover for streams where it was present</td>
<td>Stewart et al. (2019)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>N cycle</td>
<td>Lower efficiency in NO$_3$ attenuation</td>
<td>Stewart et al. (2019)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2. Effects of the colonization of conifer clear-cut areas by the native deciduous N-fixing *Alnus rubra* in western North America, assessed by the comparison between streams in old-growth conifer forests and in *A. rubra*-colonized areas, as reported in the literature.

<table>
<thead>
<tr>
<th>Stream characteristic</th>
<th>Effects of the invasion (response in invaded compared with non-invaded condition)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stream N concentrations</td>
<td>Positive relationship between nitrate and dissolved organic N concentrations with percentage broadleaf cover; relationship stronger with percentage cover within the entire watershed than in the riparian area only Higher nitrate and total N concentrations No effect of invasion on N concentrations</td>
<td>Compton <em>et al</em>. (2003); Volk <em>et al</em>. (2003); Kominoski <em>et al</em>. (2011)</td>
</tr>
<tr>
<td>Stream discharge</td>
<td>Potentially lower given the higher transpiration in riparian forests invaded by <em>A. rubra</em> that constitute young-aged stands compared with old-growth conifer forests</td>
<td>Moore <em>et al</em>. (2004)</td>
</tr>
<tr>
<td>Litter inputs to streams</td>
<td>Higher annual litter inputs; higher N concentration in litter inputs; higher litter N fluxes to streams</td>
<td>Hart (2006); Volk <em>et al</em>. (2003); Kominoski <em>et al</em>. (2011)</td>
</tr>
<tr>
<td>Detritus export</td>
<td>Higher detritus export; positive relationship with percentage canopy cover by <em>A. rubra</em></td>
<td>Piccolo &amp; Wipfli (2002); Wipfli &amp; Musslewhite (2004)</td>
</tr>
<tr>
<td>Microbes associated with decomposing litter</td>
<td>Higher microbial respiration rates in deciduous than in conifer streams for <em>A. rubra</em> leaves; higher respiration rates in mixed deciduous–conifer than conifer streams for <em>Tsuga heterophylla</em> needles; no effect of litter identity or invasion on overall microbial community structure; no effect of invasion on bacterial and fungal allele diversity; higher microbial allele richness in <em>T. heterophylla</em> than <em>A. rubra</em> litter</td>
<td>Kominoski <em>et al</em>. (2011)</td>
</tr>
<tr>
<td>Macroinvertebrates associated with decomposing leaves</td>
<td>Higher biomass and abundance in <em>A. rubra</em> leaves than <em>T. heterophylla</em> needles, and higher in mixed <em>A. rubra</em>–conifer than conifer streams; no effect of invasion or litter species on taxon richness; higher taxa evenness in <em>T. heterophylla</em> than <em>A. rubra</em> litter and in conifer streams; effects of invasion and litter species on community structure</td>
<td>Kominoski <em>et al</em>. (2011)</td>
</tr>
<tr>
<td>Macroinvertebrates associated with decomposing wood</td>
<td>Higher total density and biomass; higher relative biomass of collector-gatherers and collector-filterers and lower relative biomass of scrapers and shredders; no effect of invasion on diversity</td>
<td>Kimbirauskas <em>et al</em>. (2008)</td>
</tr>
<tr>
<td>Macroinvertebrate export</td>
<td>Higher export (number and biomass); positive relationship with percentage canopy cover by <em>A. rubra</em></td>
<td>Piccolo &amp; Wipfli (2002); Wipfli &amp; Musslewhite (2004)</td>
</tr>
<tr>
<td>Litter decomposition</td>
<td>Positive relationship between total decomposition rates of <em>A. rubra</em></td>
<td>Kominoski <em>et al</em>. (2011)</td>
</tr>
</tbody>
</table>
*rubra* leaves and percentage riparian cover by deciduous species; no effect of invasion on total decomposition rates of *T. heterophylla* needles or on microbially driven decomposition rates of both litter species.
Table 3. List of countries (and regions) where *Acacia dealbata* and *Acacia melanoxylon* are reported as invasive. Countries with more information (studies) on *Acacia dealbata* and *Acacia melanoxylon* invasiveness are marked with an asterisk.

<table>
<thead>
<tr>
<th>Country/Region</th>
<th>Acacia dealbata</th>
<th>Acacia melanoxylon</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>North America</strong></td>
<td>X</td>
<td>X</td>
<td>Rejmánek &amp; Richardson (2013)</td>
</tr>
<tr>
<td>USA</td>
<td>X</td>
<td>X</td>
<td>Swearingen &amp; Bargeron (2016); Randall (2017); CABI (2019)</td>
</tr>
<tr>
<td><strong>Central America</strong></td>
<td></td>
<td></td>
<td>Rejmánek &amp; Richardson (2013)</td>
</tr>
<tr>
<td>Mexico</td>
<td>X</td>
<td></td>
<td>CONABIO (2018)</td>
</tr>
<tr>
<td><strong>South America</strong></td>
<td>X</td>
<td>X</td>
<td>Rejmánek &amp; Richardson (2013)</td>
</tr>
<tr>
<td>Argentina</td>
<td>X</td>
<td>X</td>
<td>Zalba &amp; Villamil (2002); Fonseca <em>et al.</em> (2013)</td>
</tr>
<tr>
<td>Brazil</td>
<td></td>
<td>X</td>
<td>Fonseca <em>et al.</em> (2013)</td>
</tr>
<tr>
<td>Chile*</td>
<td>X</td>
<td>X</td>
<td>Fuentes <em>et al.</em> (2010); Fuentes-Ramírez <em>et al.</em> (2011); CABI (2019)</td>
</tr>
<tr>
<td>Colombia</td>
<td></td>
<td>X</td>
<td>Randall (2017)</td>
</tr>
<tr>
<td>Uruguay</td>
<td>X</td>
<td></td>
<td>Masciadri <em>et al.</em> (2010)</td>
</tr>
<tr>
<td><strong>Atlantic Islands</strong></td>
<td></td>
<td>X</td>
<td>Rejmánek &amp; Richardson (2013)</td>
</tr>
<tr>
<td><strong>Europe</strong></td>
<td>X</td>
<td>X</td>
<td>Rejmánek &amp; Richardson (2013)</td>
</tr>
<tr>
<td>Algeria</td>
<td>X</td>
<td>X</td>
<td>CABI (2019)</td>
</tr>
<tr>
<td>France</td>
<td>X</td>
<td>X</td>
<td>Lorenzo <em>et al.</em> (2010); Ducatillion <em>et al.</em> (2015)</td>
</tr>
<tr>
<td>Italy</td>
<td>X</td>
<td></td>
<td>Celesti-Grapow <em>et al.</em> (2009); Lorenzo <em>et al.</em> (2010)</td>
</tr>
<tr>
<td>Portugal*</td>
<td>X</td>
<td>X</td>
<td>Marchante <em>et al.</em> (2014)</td>
</tr>
<tr>
<td>Spain*</td>
<td>X</td>
<td>X</td>
<td>Sanz-Elorza <em>et al.</em> (2004); Lorenzo <em>et al.</em> (2010)</td>
</tr>
<tr>
<td>Switzerland</td>
<td>X</td>
<td></td>
<td>Schoenenberger <em>et al.</em> (2014)</td>
</tr>
<tr>
<td>Turkey</td>
<td>X</td>
<td></td>
<td>Atasoy &amp; Çorbacı (2018)</td>
</tr>
<tr>
<td><strong>Africa (southern)</strong></td>
<td>X</td>
<td>X</td>
<td>Rejmánek &amp; Richardson (2013)</td>
</tr>
<tr>
<td>South Africa*</td>
<td>X</td>
<td>X</td>
<td>Henderson (1992); van Wilgen &amp; Wilson (2018)</td>
</tr>
<tr>
<td>Swaziland</td>
<td>X</td>
<td>X</td>
<td>Swaziland National Trust Commission (2019)</td>
</tr>
<tr>
<td><strong>Africa (central)</strong></td>
<td></td>
<td>X</td>
<td>Rejmánek &amp; Richardson (2013)</td>
</tr>
<tr>
<td>Congo</td>
<td>X</td>
<td>X</td>
<td>Mbale (2010); Randall (2017)</td>
</tr>
<tr>
<td>Ethiopia</td>
<td>X</td>
<td></td>
<td>Randall (2017)</td>
</tr>
<tr>
<td>Tanzania</td>
<td>X</td>
<td></td>
<td>CABI (2019)</td>
</tr>
<tr>
<td><strong>Asia</strong></td>
<td></td>
<td>X</td>
<td>Rejmánek &amp; Richardson (2013)</td>
</tr>
<tr>
<td>Bhutan</td>
<td>X</td>
<td></td>
<td>Sankaran &amp; Suresh (2013)</td>
</tr>
<tr>
<td>Country</td>
<td>X</td>
<td>X</td>
<td>References</td>
</tr>
<tr>
<td>-------------------------</td>
<td>---</td>
<td>---</td>
<td>------------------------------------------------</td>
</tr>
<tr>
<td>China</td>
<td>X</td>
<td>X</td>
<td>Axmacher &amp; Sang (2013); Sankaran &amp; Suresh (2013)</td>
</tr>
<tr>
<td>India</td>
<td>X</td>
<td>X</td>
<td>Sankaran &amp; Suresh (2013); Sekar (2015); Randall (2017); CABI (2019)</td>
</tr>
<tr>
<td>Israel</td>
<td>X</td>
<td>X</td>
<td>Dufour-Dror (2013)</td>
</tr>
<tr>
<td>Sri Lanka</td>
<td>X</td>
<td>X</td>
<td>Sankaran &amp; Suresh (2013); CABI (2019)</td>
</tr>
<tr>
<td>Thailand</td>
<td>X</td>
<td></td>
<td>Sankaran &amp; Suresh (2013)</td>
</tr>
<tr>
<td><strong>Indian Ocean Islands</strong></td>
<td>X</td>
<td></td>
<td>Rejmánek &amp; Richardson (2013)</td>
</tr>
<tr>
<td>Madagascar</td>
<td>X</td>
<td></td>
<td>Binggeli (2003)</td>
</tr>
<tr>
<td>Reunion Island</td>
<td>X</td>
<td></td>
<td>Tassin <em>et al.</em> (2006)</td>
</tr>
<tr>
<td><strong>Australia</strong></td>
<td>X</td>
<td>X</td>
<td>Rejmánek &amp; Richardson (2013)</td>
</tr>
<tr>
<td><strong>Pacific Islands</strong></td>
<td>X</td>
<td></td>
<td>Rejmánek &amp; Richardson (2013)</td>
</tr>
<tr>
<td>Hawaii</td>
<td>X</td>
<td></td>
<td>CABI (2019)</td>
</tr>
<tr>
<td>Japan</td>
<td>X</td>
<td></td>
<td>Sankaran &amp; Suresh (2013)</td>
</tr>
<tr>
<td>New Caledonia</td>
<td>X</td>
<td></td>
<td>Sankaran &amp; Suresh (2013)</td>
</tr>
<tr>
<td>New Zealand*</td>
<td>X</td>
<td>X</td>
<td>Howell (2008); CABI (2019)</td>
</tr>
<tr>
<td>Taiwan</td>
<td>X</td>
<td></td>
<td>EFlora.org (2015)</td>
</tr>
</tbody>
</table>
Table 4. Distribution and characterization of alien and native tree species from the perspective of stream ecosystems in Portugal. The native species co-occur and their traits are complementary in maintaining stream functioning, e.g. the different decomposition rates of native leaf litter ensures that there will be litter in the stream bed from autumn to spring. Key references: Schindler & Gessner (2009), Ferreira et al. (2012), Graça & Poquet (2014), Jabiol et al. (2019), CABI (2019) and https://jb.utad.pt (last accessed on 5 November 2019).

<table>
<thead>
<tr>
<th>Distribution and tree characteristics most relevant for streams</th>
<th>Consequences of tree characteristics for streams</th>
<th>Acacia dealbata (silver wattle)</th>
<th>Acacia melanoxylon (Australian backwood)</th>
<th>Quercus robur (common oak)</th>
<th>Castanea sativa (sweet chestnut)</th>
<th>Salix atrocinerea (grey willow)</th>
<th>Salix caprea</th>
<th>Populus nigra (black poplar)</th>
<th>Fraxinus angustifolia (narrow-leaved ash)</th>
<th>Alnus glutinosa (common alder)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Native range</td>
<td>–</td>
<td>South-eastern Australia</td>
<td>South-eastern Australia</td>
<td>Most of Europe west of the Caucasus</td>
<td>Europe and Asia Minor</td>
<td>Atlantic regions of Europe and North Africa and some Mediterranean islands</td>
<td>Most of Europe, southwest and central Asia and northwest Africa</td>
<td>Entire country</td>
<td>Central and southern Europe, northwest Africa, and southwest Asia</td>
<td>Most of Europe, southwest Asia and northern Africa</td>
</tr>
<tr>
<td>Range in Portugal</td>
<td>–</td>
<td>Entire country</td>
<td>Entire country</td>
<td>Most in central and northern Portugal</td>
<td>Entire country</td>
<td>Entire country</td>
<td>Entire country</td>
<td>Entire country</td>
<td>Entire country</td>
<td>Entire country except interior south</td>
</tr>
<tr>
<td>Status in Portugal</td>
<td>–</td>
<td>Invasive alien</td>
<td>Invasive alien</td>
<td>Native</td>
<td>Native</td>
<td>Native</td>
<td>Native</td>
<td>Native</td>
<td>Native</td>
<td>Native</td>
</tr>
<tr>
<td>Deciduousness</td>
<td>Regulates litter fall dynamics and water availability due to transpiration dynamics</td>
<td>Evergreen</td>
<td>Evergreen</td>
<td>Deciduous</td>
<td>Deciduous</td>
<td>Deciduous</td>
<td>Deciduous</td>
<td>Deciduous</td>
<td>Deciduous</td>
<td>Deciduous</td>
</tr>
<tr>
<td>Seasonality</td>
<td>Autumnal litter fall sustains aquatic food webs that have their life cycles synchronized with litter fall</td>
<td>Year round</td>
<td>Year round</td>
<td>Winter</td>
<td>Autumn</td>
<td>Early autumn</td>
<td>Early autumn</td>
<td>Autumn</td>
<td>Autumn</td>
<td>Autumn</td>
</tr>
</tbody>
</table>

62
<table>
<thead>
<tr>
<th>N-fixer</th>
<th>Fast growth rates may lead to the fast production of high amounts of litter</th>
<th>Yes</th>
<th>Yes</th>
<th>No</th>
<th>No</th>
<th>No</th>
<th>No</th>
<th>No</th>
<th>Yes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Growth rate</td>
<td>N-fixing trees may increase water nutrient concentration and N concentration of litter fall</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Longevity</td>
<td>Fast growth rates may lead to the fast production of high amounts of litter</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Root system</td>
<td>Long life forms are more efficient in stabilizing stream margins</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Leaf shape and size</td>
<td>Long life forms are more efficient in stabilizing stream margins</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Leaf litter quality</td>
<td>Long life forms are more efficient in stabilizing stream margins</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
</tr>
</tbody>
</table>

**Phenology**

- **N-fixer:**
  - N-fixing trees may increase water nutrient concentration and N concentration of litter fall.
- **Growth rate:**
  - Fast growth rates may lead to the fast production of high amounts of litter.
- **Longevity:**
  - Long life forms are more efficient in stabilizing stream margins.
- **Root system:**
  - Well-developed, extensive root systems that tolerate flooding contribute to sustain stream margins; woody adventitious roots are also important habitats for aquatic invertebrates.
- **Leaf shape and size:**
  - Entire and large leaves are better retained in the stream reach.
- **Leaf litter quality:**
  - Soft and nutrient-rich leaf litter is colonized and decomposed faster than more recalcitrant leaf litter; recalcitrant leaf litter sustains.

**Leaf litter quality**

- **Soft and nutrient-rich leaf litter:**
  - Decomposed faster than more recalcitrant leaf litter.
  - Recalcitrant leaf litter sustains.
  - Low lignin:N; High lignin:N; High polyphenol concentrations.
  - High lignin:N; High polyphenol concentrations.

**Leaf shape and size**

- **Entire and large leaves:**
  - Are better retained in the stream reach.

**Root system**

- **Well-developed:**
  - Extensive and superficial root systems.
  - Tolerates flooding.
  - Robust, very expansive but shallow; It does not resist soaking.
  - Extensive; needs permanent soil humidity; tolerates flooding.
  - Lateral, shallow or deep, very vigorous and invasive.
  - Main root tending to penetrate but with superficial lateral roots.
  - Superficial and well developed; roots need to be in almost permanent contact with the water table; tolerates flooding.

**Leaf shape and size**

- **Entire medium-sized leaf:**
  - With large number of very small leaflets.
  - Entire small-sized leaf.
  - Entire medium-sized leaf.
  - Entire small-sized leaf.
  - Entire medium-sized leaf.

**Leaf litter quality**

- **Entire small-sized leaf:**
  - With large number of very small leaflets.
  - Entire medium-sized leaf.
  - Entire large-sized leaf.
  - Entire small-sized leaf.
  - Entire medium-sized leaf.

**Leaf litter quality**

- **Entire medium-sized leaf:**
  - With large number of very small leaflets.
  - Entire medium-sized leaf.
  - Entire large-sized leaf.
  - Entire small-sized leaf.
  - Entire medium-sized leaf.

**Leaf litter quality**

- **Entire large-sized leaf:**
  - With large number of very small leaflets.
  - Entire medium-sized leaf.
  - Entire large-sized leaf.
  - Entire small-sized leaf.
  - Entire medium-sized leaf.

**Leaf litter quality**

- **Entire large-sized leaf:**
  - With large number of very small leaflets.
  - Entire medium-sized leaf.
  - Entire large-sized leaf.
  - Entire small-sized leaf.
  - Entire medium-sized leaf.

**Leaf litter quality**

- **Entire large-sized leaf:**
  - With large number of very small leaflets.
  - Entire medium-sized leaf.
  - Entire large-sized leaf.
  - Entire small-sized leaf.
  - Entire medium-sized leaf.

**Leaf litter quality**

- **Entire large-sized leaf:**
  - With large number of very small leaflets.
  - Entire medium-sized leaf.
  - Entire large-sized leaf.
  - Entire small-sized leaf.
  - Entire medium-sized leaf.

**Leaf litter quality**

- **Entire large-sized leaf:**
  - With large number of very small leaflets.
  - Entire medium-sized leaf.
  - Entire large-sized leaf.
  - Entire small-sized leaf.
  - Entire medium-sized leaf.

**Leaf litter quality**

- **Entire large-sized leaf:**
  - With large number of very small leaflets.
  - Entire medium-sized leaf.
  - Entire large-sized leaf.
  - Entire small-sized leaf.
  - Entire medium-sized leaf.

**Leaf litter quality**

- **Entire large-sized leaf:**
  - With large number of very small leaflets.
  - Entire medium-sized leaf.
  - Entire large-sized leaf.
  - Entire small-sized leaf.
  - Entire medium-sized leaf.

**Leaf litter quality**

- **Entire large-sized leaf:**
  - With large number of very small leaflets.
  - Entire medium-sized leaf.
  - Entire large-sized leaf.
  - Entire small-sized leaf.
  - Entire medium-sized leaf.

**Leaf litter quality**

- **Entire large-sized leaf:**
  - With large number of very small leaflets.
  - Entire medium-sized leaf.
  - Entire large-sized leaf.
  - Entire small-sized leaf.
  - Entire medium-sized leaf.

**Leaf litter quality**

- **Entire large-sized leaf:**
  - With large number of very small leaflets.
  - Entire medium-sized leaf.
  - Entire large-sized leaf.
  - Entire small-sized leaf.
  - Entire medium-sized leaf.

**Leaf litter quality**

- **Entire large-sized leaf:**
  - With large number of very small leaflets.
  - Entire medium-sized leaf.
  - Entire large-sized leaf.
  - Entire small-sized leaf.
  - Entire medium-sized leaf.

**Leaf litter quality**

- **Entire large-sized leaf:**
  - With large number of very small leaflets.
  - Entire medium-sized leaf.
  - Entire large-sized leaf.
  - Entire small-sized leaf.
  - Entire medium-sized leaf.

**Leaf litter quality**

- **Entire large-sized leaf:**
  - With large number of very small leaflets.
  - Entire medium-sized leaf.
  - Entire large-sized leaf.
  - Entire small-sized leaf.
  - Entire medium-sized leaf.

**Leaf litter quality**

- **Entire large-sized leaf:**
  - With large number of very small leaflets.
  - Entire medium-sized leaf.
  - Entire large-sized leaf.
  - Entire small-sized leaf.
  - Entire medium-sized leaf.

**Leaf litter quality**

- **Entire large-sized leaf:**
  - With large number of very small leaflets.
  - Entire medium-sized leaf.
  - Entire large-sized leaf.
  - Entire small-sized leaf.
  - Entire medium-sized leaf.

**Leaf litter quality**

- **Entire large-sized leaf:**
  - With large number of very small leaflets.
  - Entire medium-sized leaf.
  - Entire large-sized leaf.
  - Entire small-sized leaf.
  - Entire medium-sized leaf.

**Leaf litter quality**

- **Entire large-sized leaf:**
  - With large number of very small leaflets.
  - Entire medium-sized leaf.
  - Entire large-sized leaf.
  - Entire small-sized leaf.
  - Entire medium-sized leaf.

**Leaf litter quality**

- **Entire large-sized leaf:**
  - With large number of very small leaflets.
  - Entire medium-sized leaf.
  - Entire large-sized leaf.
  - Entire small-sized leaf.
  - Entire medium-sized leaf.

**Leaf litter quality**

- **Entire large-sized leaf:**
  - With large number of very small leaflets.
  - Entire medium-sized leaf.
  - Entire large-sized leaf.
  - Entire small-sized leaf.
  - Entire medium-sized leaf.

**Leaf litter quality**

- **Entire large-sized leaf:**
  - With large number of very small leaflets.
  - Entire medium-sized leaf.
  - Entire large-sized leaf.
  - Entire small-sized leaf.
  - Entire medium-sized leaf.

**Leaf litter quality**

- **Entire large-sized leaf:**
  - With large number of very small leaflets.
  - Entire medium-sized leaf.
  - Entire large-sized leaf.
  - Entire small-sized leaf.
  - Entire medium-sized leaf.

**Leaf litter quality**

- **Entire large-sized leaf:**
  - With large number of very small leaflets.
  - Entire medium-sized leaf.
  - Entire large-sized leaf.
  - Entire small-sized leaf.
  - Entire medium-sized leaf.

**Leaf litter quality**

- **Entire large-sized leaf:**
  - With large number of very small leaflets.
  - Entire medium-sized leaf.
  - Entire large-sized leaf.
  - Entire small-sized leaf.
  - Entire medium-sized leaf.
| Leaf litter decomposition rate in streams | Faster decomposition may lead to the disappearance of litter from the stream | Slow-medium* | Slow** | Slow | Medium | Medium | Medium | Fast | Fast |

*anticipated decomposition rates based on soil incubations (Xiang & Bauhus, 2007; Castro-Díez et al., 2012)

**decomposition rates in invaded range (see Table 6).
Table 5. Characteristics of invasive *Acacia* species contributing to their invasive potential, possibly affecting stream ecosystems.

<table>
<thead>
<tr>
<th>Characteristics</th>
<th>Consequences</th>
<th>Key references</th>
</tr>
</thead>
<tbody>
<tr>
<td>Establish symbiotic relationships with N-fixing bacteria</td>
<td>Ability to colonize and establish in low-quality soils, which potentially alters soil and stream water characteristics</td>
<td>Le Roux <em>et al.</em> (2018)</td>
</tr>
<tr>
<td>High adaptability to different environmental conditions and to environmental change</td>
<td>Ability to establish in different environments and to establish rapidly after disturbance (e.g. flood, fire, construction works, clear-cut), making stream riparian areas highly susceptible to invasion</td>
<td>Lorenzo <em>et al.</em> (2010)</td>
</tr>
<tr>
<td>Production of large numbers of resistant seeds with easy germination that can accumulate in the soil for long periods</td>
<td>Rapid establishment of pure <em>Acacia</em> stands, especially if disturbance eliminates native vegetation, which potentially alters plant and soil communities, soil properties, and consequently stream water characteristics, aquatic communities and processes</td>
<td>Richardson &amp; Kluge (2008)</td>
</tr>
<tr>
<td>Production of allelopathic compounds that inhibit the germination of seeds from other species</td>
<td></td>
<td>Souza-Alonso <em>et al.</em> (2014a)</td>
</tr>
<tr>
<td>High growth rates and the capacity to accumulate high biomass</td>
<td></td>
<td>Le Maitre <em>et al.</em> (2011)</td>
</tr>
<tr>
<td>Resprout after cutting, fire or frost</td>
<td></td>
<td>Richardson <em>et al.</em> (2011)</td>
</tr>
</tbody>
</table>
Table 6. Decomposition rates ($k$) of leaf litter from Acacia species incubated in streams [k values were derived using the exponential negative model, except for Akanil & Middeton (1997) where the linear model was used]. Most studies addressed Acacia litter decomposition distinct from the invasion perspective, considering Acacia species because they were in the stream riparian areas or presented litter characteristics of interest. Railoun (2018) was the only study that directly addressed Acacia invasion impacts on litter decomposition by comparing near-pristine streams and streams with the riparian area invaded by Acacia mearnsii. Acacia species with phyllodes are highlighted with an asterisk.

<table>
<thead>
<tr>
<th>Acacia species</th>
<th>$k$ (day$^{-1}$)</th>
<th>Incubation conditions and location</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acacia auriculiformis</em> (earleaf acacia)</td>
<td>0.0063–0.0081</td>
<td>Air-dried senescent litter in coarse mesh bags; streams in the Western Ghat forest (India)</td>
<td>Raviraja <em>et al.</em> (1996)</td>
</tr>
<tr>
<td><em>Acacia longifolia</em> (long-leaved wattle)</td>
<td>0.52 % loss/d</td>
<td>Air-dried litter in coarse-mesh bags; stream in central Anatolia (Turkey)</td>
<td>Akanil &amp; Middeton (1997)</td>
</tr>
<tr>
<td></td>
<td>0.0083–0.0195</td>
<td>Litter in coarse-mesh bags; peri-urban stream reaches in central Portugal</td>
<td>Serra &amp; Abelho (2018)</td>
</tr>
<tr>
<td></td>
<td>0.008</td>
<td>Litter in coarse-mesh bags; peri-urban stream in central Portugal</td>
<td>Couceiro &amp; Abelho (2015)</td>
</tr>
<tr>
<td></td>
<td>0.008</td>
<td>Litter in fine-mesh bags; peri-urban stream in central Portugal</td>
<td>Couceiro &amp; Abelho (2015)</td>
</tr>
<tr>
<td><em>Acacia mearnsii</em> (black wattle)</td>
<td>0.0225–0.0241</td>
<td>Oven-dried (50ºC) senescent litter in fine-mesh bags; near-pristine streams in the Cape Floristic Region (South Africa)</td>
<td>Railoun (2018)</td>
</tr>
<tr>
<td></td>
<td>0.0216–0.0277</td>
<td>Oven-dried (50ºC) senescent litter in fine-mesh bags; invaded streams in the Cape Floristic Region (South Africa)</td>
<td>Railoun (2018)</td>
</tr>
<tr>
<td><em>Acacia melanoxylon</em> (Australian blackwood)</td>
<td>0.0040–0.0073</td>
<td>Leached and oven-dried (40 ºC) senescent litter in coarse mesh bags; stream reaches in south-eastern Australia (native range)</td>
<td>O’Keefe &amp; Lake (1987)</td>
</tr>
<tr>
<td></td>
<td>0.0026–0.0084</td>
<td>Air-dried senescent litter in packs; streams in south-eastern Australia (native range)</td>
<td>Campbell <em>et al.</em> (1992)</td>
</tr>
<tr>
<td></td>
<td>0.0037–0.0415</td>
<td>Air-dried fresh litter in packs; streams in south-eastern Australia (native range)</td>
<td>Campbell <em>et al.</em> (1992)</td>
</tr>
<tr>
<td></td>
<td>0.008–0.011</td>
<td>Air-dried senescent litter in coarse-mesh bags; insular streams (Azores)</td>
<td>Raposeiro <em>et al.</em> (2014)</td>
</tr>
<tr>
<td></td>
<td>0.006–0.007</td>
<td>Air-dried senescent litter in fine-mesh bags; insular streams (Azores)</td>
<td>Raposeiro <em>et al.</em> (2014)</td>
</tr>
<tr>
<td></td>
<td>0.0068–0.0106</td>
<td>Air-dried fresh litter in coarse-mesh bags; insular streams over a gradient of dissolved nutrients</td>
<td>Ferreira <em>et al.</em> (2016b)</td>
</tr>
<tr>
<td>Concentration</td>
<td>Description</td>
<td>Reference</td>
<td></td>
</tr>
<tr>
<td>---------------</td>
<td>-----------------------------------------------------------------------------</td>
<td>------------------------------------</td>
<td></td>
</tr>
<tr>
<td>0.0064–0.0102</td>
<td>Air-dried fresh litter in fine-mesh bags; insular streams over a gradient of dissolved nutrients (Azores)</td>
<td>Ferreira et al. (2016b)</td>
<td></td>
</tr>
<tr>
<td>0.0047</td>
<td>Air-dried fresh litter in coarse-mesh bags; insular stream (Azores)</td>
<td>Raposeiro et al. (2018)</td>
<td></td>
</tr>
<tr>
<td>0.0053</td>
<td>Air-dried fresh litter in fine-mesh bags; insular stream (Azores)</td>
<td>Raposeiro et al. (2018)</td>
<td></td>
</tr>
</tbody>
</table>
Table 7. Stream ecosystem services that may be affected by the invasion of temperate deciduous forests by *Acacia* species. $\Delta$ denotes change (with magnitude and direction depending on effects of *Acacia* invasion) and $\downarrow$ denotes decrease.

<table>
<thead>
<tr>
<th>Type of ecosystem service</th>
<th>Ecosystem service potentially affected by <em>Acacia</em> invasion (direction of change)</th>
<th>Cause of change in ecosystem services resulting from <em>Acacia</em> invasion</th>
</tr>
</thead>
<tbody>
<tr>
<td>Provisioning (supply of goods or services)</td>
<td>Good quality water ($\downarrow$)</td>
<td>Decrease in water quantity and quality</td>
</tr>
<tr>
<td></td>
<td>Energy production ($\downarrow$)</td>
<td>Decrease in water quantity</td>
</tr>
<tr>
<td></td>
<td>Food production (e.g. fish) ($\Delta$)</td>
<td>Changes in productivity resulting from changes in food webs and processes</td>
</tr>
<tr>
<td></td>
<td>Biodiversity (e.g. genetic resources) ($\downarrow$)</td>
<td>Decrease in diversity of litter inputs and environmental conditions</td>
</tr>
<tr>
<td>Regulating (non-material benefits)</td>
<td>Litter decomposition and nutrient cycling ($\Delta$)</td>
<td>Changes in water quantity and quality, in litter inputs and in aquatic communities</td>
</tr>
<tr>
<td></td>
<td>Habitat maintenance ($\Delta$)</td>
<td>Input of large amounts of woody material</td>
</tr>
<tr>
<td></td>
<td>Water purification ($\downarrow$)</td>
<td>Decrease in water quality</td>
</tr>
<tr>
<td></td>
<td>Erosion control ($\downarrow$)</td>
<td><em>Acacia</em> tree fall and increase in sediment load</td>
</tr>
<tr>
<td></td>
<td>Climate regulation ($\Delta$)</td>
<td>Increase in transpiration due to dense stands of fast-growing, evergreen <em>Acacia</em> trees; changes in litter decomposition and CO$_2$ evasion from streams</td>
</tr>
<tr>
<td></td>
<td>Carbon and nitrogen sequestration ($\Delta$)</td>
<td>Changes in litter decomposition and in incorporation of carbon and nitrogen into food webs due to changes in water quality and litter characteristics</td>
</tr>
<tr>
<td>Supporting (services needed to support other services)</td>
<td>Biodiversity ($\downarrow$)</td>
<td>Decrease in diversity of litter inputs and environmental conditions</td>
</tr>
<tr>
<td></td>
<td>Nutrient cycling ($\Delta$)</td>
<td>Changes in litter decomposition</td>
</tr>
<tr>
<td>Cultural and life-enhancing</td>
<td>Aesthetic enjoyment ($\Delta$)</td>
<td>Loss of autumnal colours from native vegetation and effusive blooming of <em>Acacia</em> flowers in late winter</td>
</tr>
<tr>
<td></td>
<td>Recreation: swimming pools ($\downarrow$)</td>
<td>Decrease in water quantity</td>
</tr>
<tr>
<td></td>
<td>Recreation: fishing ($\Delta$)</td>
<td>Changes in productivity</td>
</tr>
<tr>
<td></td>
<td>Recreation: biodiversity ($\downarrow$)</td>
<td>Decrease in diversity of litter inputs and environmental conditions</td>
</tr>
<tr>
<td></td>
<td>Science and education ($\Delta$)</td>
<td>Changes in vegetation context with all associated changes</td>
</tr>
</tbody>
</table>
**Fig. 1.** Typical streams in central Portugal flow through deciduous broadleaf forests where *Alnus glutinosa, Salix* spp., *Populus* spp., *Fraxinus angustifolia* and *Frangula alnus* dominate the riparian vegetation as illustrated for the Ceira River, Cavaleiros de Baixo, in spring 2017 (©Sónia Serra) (A), Freixo Stream, Folgosinho, in autumn 2011 (©Raquel Calapez) (B), and Cerdeira Stream, Lousã Mountain, in winter 2019 (©Verónica Ferreira) (C).
**Fig. 2.** The extent of the invasion by *Acacia dealbata* in Lousã Mountain, central Portugal, is particularly evident between January and March when the bright yellow flowers are visible (A, B). Often, *Acacia* trees are present on the stream banks where they replace the native riparian vegetation as illustrated for São João stream, Lousã Mountain (C). Photographs taken in February 2017 (©Andreia Ferreira).
Fig. 4. Conceptual model of possible effects of the invasion of temperate deciduous broadleaf forests by N-fixing species on stream communities and processes. Δ denotes change, ↑ denotes increase, ↓ denotes decrease and ? denotes unknown direction of the expected effects.
**Fig. 5.** The contribution of *Acacia* pods (the reddish litter on the forest floor and collecting net) to litter inputs to streams flowing through *Acacia* stands is high during summer (A), and these streams also accumulate large amounts of woody material (B) as illustrated for Sotão stream, central Portugal. Photographs taken in July 2019 (©Manuel A.S. Graça).
Fig. 6. Conceptual framework to predict effects of invasion of temperate deciduous broadleaf forests by N-fixing species on streams by considering a continuum from early to advanced stages of invasion by N-fixing species (e.g. Acacia spp.) of deciduous forests with (i) low and (ii) high representation of N-fixing species in the riparian area. Deciduous forests with low representation of N-fixing species are dominated by Salix spp. but have low cover of Alnus glutinosa, while forests with high representation of N-fixing species are dominated by A. glutinosa. Changes are predicted for riparian tree species richness (A), cover of N-fixing species (B), water N concentrations (C), stream discharge (D), and litter decomposition potential (i.e. overall litter decomposition rate) where effects mediated by increased water nutrient concentrations prevail (E) and where effects mediated by increased recalcitrance of organic matter inputs prevail (F).