

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

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15

16 **ABSTRACT**

17 Biological invasions are a major threat to biodiversity and ecosystem functioning. Forest
18 invasion by alien woody species can have cross-ecosystem effects. This is especially relevant in the
19 case of stream–riparian forest meta-ecosystems as forest streams depend strongly on riparian
20 vegetation for carbon, nutrients and energy. Forest invasion by woody species with dissimilar
21 characteristics from native species may be particularly troublesome. The invasion of temperate
22 deciduous broadleaf forests with low representation of nitrogen (N)-fixing species by N-fixers has
23 the potential to induce ecosystem changes at the stream level. Although effects of tree invasion on
24 stream ecosystems have been under assessed, knowledge of native and invasive tree characteristics
25 allows prediction of invasion effects on streams. Here we present a conceptual model to predict the

26 effects of forest invasion by alien N-fixing species on streams, using as a background the invasion
27 of temperate deciduous broadleaf forests by leguminous *Acacia* species, which are among the most
28 aggressive invaders worldwide. Effects are discussed using a trait-based approach to allow the
29 model to be applied to other pairs of invaded ecosystem–invasive species, taking into account
30 differences in species traits and environmental conditions. Anticipated effects of N-fixing species
31 invasions include changes in water quality (increase in N concentration) and quantity (decrease in
32 flow) and changes in litter input characteristics (altered diversity, seasonality, typology, quantity
33 and quality). The magnitude of these changes will depend on the magnitude of differences in
34 species traits, the extent and duration of the invasion and stream characteristics (e.g. basal nutrient
35 concentration). The extensive literature on effects of nutrient enrichment of stream water, water
36 scarcity and changes in litter input characteristics on aquatic communities and processes allows
37 prediction of invasion effects on stream structure and function. The magnitude of invasion effects
38 on aquatic communities and processes may, however, depend on interactions among different
39 pathways (e.g. effects mediated by increases in stream nutrient concentration may contrast with
40 those mediated by decreases in water availability or by decreases in litter nutritional quality). A
41 review of the literature addressing effects of increasing cover of N-fixing species on streams
42 suggests a wide application of the model, while it highlights the need to consider differences in the
43 type of system and species when making generalizations. Changes induced by N-fixing species
44 invasion on streams can jeopardize multiple ecosystem services (e.g. good quality water,
45 hydroelectricity, leisure activities), with relevant social and economic consequences.

46

47 *Key words:* *Acacia*, alien tree species, conceptual model, forest change, litter decomposition, stream
48 communities.

49

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81 I. INTRODUCTION

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

95 Riparian vegetation is one of the most important factors controlling in-stream functioning: it
96 provides shade, thus reducing the amount of solar radiation reaching the stream bed and controlling
97 water temperature, which limits in-stream primary production; it provides organic matter as a food
98 source and substrate for aquatic organisms; it provides habitat for aquatic organisms (e.g.
99 submerged roots, branches and logs); it stabilizes the banks, limiting erosion and the input of fine
100 sediments; and it also buffers the impact of human activities, such as forestry, agriculture or
101 urbanization, on streams (e.g. by reducing the input of nutrients and pesticides) (Cummins *et al.*,
102 1989; Wenger, 1999; Dosskey *et al.*, 2010; Tolkkinen *et al.*, 2020). However, given their position in
103 the interface between the aquatic and terrestrial environments, riparian forests are one of the most

104 susceptible habitats to species invasions, especially in landscapes highly disturbed by human
105 activities (Pyšek *et al.*, 2010), and are listed among the most invaded habitats (Richardson *et al.*,
106 2007). On one hand, stream hydrologic dynamics are, by nature, a source of disturbance for riparian
107 areas (e.g. spates and floods), making them susceptible to invasions (Lewerentz *et al.*, 2019).
108 Streams can also act as corridors for invasions by carrying plant propagules downstream and
109 sideways (e.g. during floods) (Cabra-Rivas, Alonso & Castro-Díez, 2014; Catford & Jansson, 2014;
110 Kuglerová *et al.*, 2015; Čuda *et al.*, 2017). On the other hand, human activities such as forestry,
111 agriculture and urbanization often compete for space with riparian forests leading to their
112 degradation (Pennington, Hansel & Gorchoy, 2010). Additionally, because human activities are the
113 primary cause of the introduction (intentional or accidental) of alien species, the proximity of these
114 activities to riparian forests increases their exposure to biological invasions (Sanz-Elorza, Dana &
115 Sobrino, 2006; Giorgis *et al.*, 2011; Spear *et al.*, 2013).

116 The effects of invasion by alien riparian tree species on stream ecosystems may be stronger
117 when invasive and native species are functionally different (Kominoski *et al.*, 2013; Castro-Díez *et*
118 *al.*, 2014; Le Maitre, Gush & Dzikiti, 2015). In particular, the arrival of alien nitrogen (N)-fixing
119 woody species to riparian habitats where this functional trait is underrepresented or absent may
120 have significant effects on stream functioning, as suggested by two meta-analyses on the effects of
121 plant invasions on terrestrial ecosystems (Liao *et al.*, 2008; Castro-Díez *et al.*, 2014). Liao *et al.*
122 (2008) found stronger influences on N cycles of invasions by N-fixing than by non-N-fixing species
123 and Castro-Díez *et al.* (2014) found that alien plant invasions alter N cycles especially when
124 invasive and native species differ in their N-fixing ability. The magnitude of the effects may
125 increase with the establishment of monospecific stands of the invasive species, which reduces
126 compositional and functional plant diversity and redundancy (Kominoski *et al.*, 2013), leading to
127 the creation of novel riparian ecosystems (Catford *et al.*, 2013). Also, changes in ecosystem
128 structure and function may be stronger in the case of long-term than more recent invasions
129 (Marchante *et al.*, 2008, 2015; Souza-Alonso, Guisande-Collazo & González, 2015). With invasion

130 time, the reversibility of the effects also decreases, making recovery more difficult (Le Maitre *et al.*,
131 2011).

132 Invasions by alien N-fixing woody species are a global problem. Richardson & Rejmánek
133 (2011) identified 131 N-fixing tree and shrub species (legumes plus actinorhizal species) that are
134 invasive in at least one region, representing 21% of the total number of invasive alien tree and shrub
135 species worldwide. Castro-Díez & Alonso (2017) listed 12 alien tree species invading riparian areas
136 in the Iberian Peninsula, 50% of which are N-fixing species. Understanding how streams function
137 under invaded riparian forests is crucial to foresee invasion impacts on stream ecosystem services,
138 which are disproportionally numerous and vital taking into account the small area streams occupy
139 globally (Capon *et al.*, 2013). However, despite the high number of invasive alien N-fixing woody
140 species, studies addressing their effects on stream ecosystems are scarce.

141

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

143 Existing studies have addressed the in-stream effects of invasion by alien species such as
144 *Acacia mearnsii* in South Africa, *Elaeagnus angustifolia* in the western USA, *Elaeagnus umbellata*
145 in the eastern USA, *Falcataria moluccana* in Hawaii and *Ulex europaeus* in New Zealand (Table
146 1). Despite the small number of studies, and differences in the identity and functional type of the
147 invasive species and in the type of the invaded ecosystem, it emerges as a general trend that the
148 invasion of riparian areas by N-fixing species leads to higher N concentrations in stream water and
149 sediments (Goldstein, Williard & Schoonover *et al.*, 2009; Atwood *et al.*, 2010; Mineau, Baxter &
150 Marcarelli, 2011; Wiegner *et al.*, 2013; Stewart *et al.*, 2019) and lower N limitation of biofilms
151 (Mineau *et al.*, 2011; Wiegner *et al.*, 2013). Changes in litter inputs (Mineau *et al.*, 2012; Railoun,
152 2018), the N cycle (Mineau *et al.*, 2011; Stewart *et al.*, 2019), benthic invertebrate communities
153 (Lowe *et al.*, 2008) and food webs (Atwood *et al.*, 2010) have also been reported (Table 1).

154 Despite our focus on invasion by alien N-fixing species, studies addressing the colonization
155 and expansion of native N-fixing species are also relevant in the present context. The colonization

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

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

178 Comparison of studies addressing the increase in cover by N-fixing species (native or alien)
179 suggests that extrapolations to other situations need to consider differences in the invaded systems
180 and invasive species. For instance, effects may differ when conifer forests are colonized or invaded
181 by deciduous N-fixing species (e.g. *A. rubra*) and when deciduous broadleaf forests are colonized

182 or invaded by evergreen alien N-fixing species (e.g. *Acacia* species). The large number of invasive
183 and potentially invasive N-fixing species that could significantly change stream–riparian forest
184 meta-ecosystems and the large areas they have already invaded (Richardson & Rejmánek, 2011)
185 make the understanding of their effects urgent. This is especially important given that mitigating N
186 enrichment of freshwater ecosystems is a major conservation challenge (Vitousek *et al.*, 1997;
187 Carpenter, Stanley & Vander-Zanden, 2011), and the effects of invasive N-fixing species have been
188 largely overlooked in this context.

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

200

201 **III. THE INVASION OF TEMPERATE DECIDUOUS BROADLEAF FORESTS BY**

202 **ACACIA SPECIES**

203 **(1) Temperate deciduous broadleaf forests and their streams**

204 In the northern hemisphere, typical dominant trees in temperate deciduous broadleaf forests
205 (‘deciduous forests’ hereafter) include species of, e.g. *Quercus*, *Acer*, *Fagus*, *Betula*, *Ulmus* and
206 *Tilia*. In mainland Portugal, deciduous forests predominate in the central and northern regions and
207 are typically composed of a species mixture, with major contributors being *Quercus* spp., *Castanea*

208 *sativa*, *Prunus* spp. and *Ulmus* spp., very often including evergreen elements (e.g. *Ilex aquifolium*,
209 *Arbutus unedo*, *Laurus nobilis*, *Viburnum tinus*, *Phyllirea* spp.) (Costa *et al.*, 1998). In riparian
210 areas, common species include *Alnus glutinosa*, *Salix* spp., *Populus* spp., *Fraxinus angustifolia* and
211 *Frangula alnus* (Table 4). Of these species, *A. glutinosa* is an actinorhizal species that establishes
212 symbiosis with the N-fixing actinobacteria *Frankia alni*, thus acting as an N-fixing tree species
213 (Table 4). The coexistence of several tree species ensures diversity and redundancy of functional
214 traits (Table 4), a key feature to guarantee stream multifunctionality and resilience to environmental
215 changes (Kominoski *et al.*, 2013).

216 In deciduous forests, streams are shaded from mid-spring to mid-autumn (i.e. when the tree
217 canopy is fully developed; Fig. 1), which limits in-stream primary production (Bott *et al.*, 1985;
218 Alberts, Beaulieu & Buffam, 2017). In-stream primary production is also limited during the rest of
219 the year (i.e. from mid-autumn to mid-spring) due to low insolation and low water temperatures
220 (Bott *et al.*, 1985; Alberts *et al.*, 2017). Here, the riparian vegetation has a key functional role by
221 fuelling streams with large amounts of plant litter, mostly senescent leaves, which constitute the
222 primary source of carbon and energy for aquatic food webs (Abelho, 2001). Forest streams are,
223 thus, heterotrophic systems (Bott *et al.*, 1985; Hagen *et al.*, 2010; Alberts *et al.*, 2017). Litter inputs
224 to streams occur mostly during autumn/winter when deciduous tree species shed their leaves
225 (Abelho & Graça, 1996; Molinero & Pozo, 2004; Swan & Palmer, 2004). Differences in litter fall
226 phenology and in litter decomposability among tree species allow the presence of organic matter in
227 stream beds from autumn, when insect larvae start to hatch from eggs laid in summer, until spring,
228 when water temperatures start to rise and insect larvae are ready to leave the aquatic environment
229 and become winged adults (Molinero & Pozo, 2004). Streams and riparian forests are, thus, tightly
230 linked by double transfer of energy and matter (e.g. plant litter flows from the vegetation to the
231 streams, while adult invertebrates flow in the opposite direction) (Marks, 2019; Tolkkinen *et al.*,
232 2020). Therefore, streams are highly sensitive to forest changes, including changes in tree species
233 composition (Chauvet *et al.*, 2016; Ferreira *et al.*, 2016a).

234

235 **(2) Invasive behaviour of *Acacia* species**

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

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

253 *Acacia* species establish symbiotic relationships with root-nodule N-fixing bacteria (*Rhizobia*
254 spp.) (Brockwell *et al.*, 2005), which affects soil characteristics and edaphic communities
255 (Marchante *et al.*, 2008; Lorenzo *et al.*, 2010; Hellmann *et al.*, 2011; González-Muñoz, Costa-
256 Tenorio & Espigares, 2012; Lazzaro *et al.*, 2014; Souza-Alonso, Novoa & González, 2014b), and
257 facilitates *Acacia* species colonization of nutrient-poor soils (Table 5). The large number of invasive
258 *Acacia* species and their wide ecological range enable them to establish in different habitats,
259 including riparian areas (Table 5). Invasive *Acacia* species worldwide, e.g. *A. dealbata*, *A.*

260 *melanoxyton*, *Acacia longifolia*, *Acacia mangium* and *Acacia saligna*, are mainly fast-growing
261 species that out-compete native species (Le Maitre *et al.*, 2011; Richardson, Roux & Wilson, 2015;
262 Table 5). As the invasion progresses, *Acacia* cover and dominance increase, leading to a decrease in
263 the richness and diversity of the native vegetation (Holmes & Cowling, 1997; Marchante,
264 Marchante & Freitas, 2003; Fuentes-Ramírez *et al.*, 2010; Hellmann *et al.*, 2011; Le Maitre *et al.*,
265 2011; González-Muñoz *et al.*, 2012; Lorenzo *et al.*, 2012; Marchante *et al.*, 2015) and of other
266 trophic levels (e.g. gallers, their parasitoids and inquiline species; López-Núñez *et al.*, 2017).
267 Additionally, some species (e.g. *A. dealbata*, *A. melanoxyton* and *A. mearnsii*) can resprout and
268 coppice with great vigour after cutting or a fire, re-invading the cleared areas very rapidly (Lorenzo
269 *et al.*, 2010; Vazquez-de-la-Cueva, 2014). Moreover, *Acacia* species produce numerous seeds that
270 are viable for long periods and accumulate in long-lasting soil seedbanks (Richardson & Kluge,
271 2008; Gibson *et al.*, 2011), which germinate after fire or clearing associated with control activities
272 or other disturbance events. Several *Acacia* species produce allelopathic compounds, which may
273 inhibit the germination of seeds or growth of other species (Souto *et al.*, 2001; Lorenzo *et al.*, 2010,
274 2011), although the role of allelopathy in the process of invasion has been considered mostly
275 negligible under field conditions (Souza-Alonso *et al.*, 2017). These characteristics allow *Acacia*
276 species to be successful invaders in many areas, including riparian areas, forming (nearly)
277 monospecific stands, altering the landscape and ecosystem services (Table 5; Fig. 2).

278

279 **(3) Streams as invasion corridors**

280 The spread of invasive plant species is often promoted by corridors, which are more effective
281 if their spatial structure is based on a dense and connected network, such as streams and roads
282 (Procheş *et al.*, 2005; Christen & Matlack, 2006). Thus, connectivity in the landscape is a major
283 driver of invasion (Procheş *et al.*, 2005), with dispersal corridors promoting and determining the
284 path of invasion (Wang *et al.*, 2011; Vicente *et al.*, 2014). Natural disturbance events associated
285 with floods may also contribute to the role of streams as dispersal corridors (Tickner *et al.*, 2001;

286 Wang *et al.*, 2011; Čuda *et al.*, 2017). The role of such corridors is clear at the landscape scale when
287 individuals of invasive species are found in large numbers near streams, but their numbers decrease
288 as the distance from the initial propagule sources increases (Wang *et al.*, 2011; Figueiredo, 2016;
289 Oliveira-Costa *et al.*, 2016).

290 Although *Acacia* species are primarily dispersed by ants or birds, depending on the dispersal
291 system of each species, they may also be dispersed by water, especially when seeds are still inside
292 the pods, with dispersal of, for example *A. dealbata* and *A. mearnsii*, being associated with
293 watercourses in Portugal, Chile, and South Africa [Gibson *et al.* (2011) and references therein].
294 Seed dispersal by water (hydrochory) is an important dispersal mechanism for invasive riparian
295 species, with seeds travelling long distances, while their germination rates are not affected by, or
296 may even increase in, water (Kaproth & McGraw, 2008; Säumel & Kowarik, 2010; Rouifed *et al.*,
297 2011; Schiedel & Tackenberg, 2013).

298

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

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

312 perspective during the flowering period, economic activities that are still ongoing (Griffin *et al.*,
313 2011; Kull *et al.*, 2011).

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

327 In Portugal, the area dominated by *Acacia* species (e.g. *A. dealbata*, *A. melanoxylon* and *A.*
328 *longifolia*) was already ~ 2,500 ha in 1977, mostly in the central and northern regions of the
329 country, with another 95,100 ha showing scattered *Acacia* trees (Fernandes, Devy-Vareta &
330 Rangan, 2013). In 2015, the area dominated by *Acacia* species was ~ 17,000 ha, with an increase of
331 ~ 500 ha/year between 2005 and 2015 (ICNF, 2019). These figures are certainly underestimates
332 because *Acacia* trees often co-occur with other species and in areas not classified as forest. The
333 increase in *Acacia* cover over time is especially high in central and northern coastal areas, where the
334 high level of disturbance of deciduous forests, promoted by different drivers (e.g. grazing, forest
335 fires, agriculture and forestry), increased their susceptibility to invasion (Pereira & Figueiredo,
336 2015). The increase in *Acacia* cover is notorious at the landscape level, both for small and medium-
337 sized watersheds. This is the case for the Arouce River watershed (central Portugal, 73 km²), where

338 the area covered by *A. dealbata* and *A. melanoxylon* has increased from 0.7% (1965) to 12.8%
339 (2011) (Oliveira-Costa *et al.*, 2016), an expansion that is considered one of the main landscape
340 changes in this territory (Ornelas *et al.*, 2018). The increase in *Acacia* cover is also significant in
341 larger areas, such as the Ceira River watershed (central Portugal, 714 km²), where the area with a
342 significant presence of *Acacia* species increased significantly between 1977 and 2018 (Fig. 3).

343 *Acacia* species are generally (in 97% of cases) associated with degraded habitats (ICNF,
344 2019). As the germination of *Acacia* species seeds is promoted by fire (Richardson & Kluge, 2008;
345 Le Maitre *et al.*, 2011), the severe rural fires that affected central Portugal in 2017 (San-Miguel-
346 Ayanz *et al.*, 2018; Fig. 3) will likely promote an increase in the area covered by these invasive
347 species. In fact, the predicted increase in fire weather danger in Europe under climate change
348 scenarios (i.e. increase in extreme fires that destroy large areas; San-Miguel-Ayanz *et al.*, 2018)
349 may be an important driver of large-scale *Acacia* invasion. Also, habitat fragmentation, by
350 expanding the edge effect in the landscape, promotes the establishment of pioneer and fast-growing
351 species, which frequently are invasive species (With, 2004).

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

363

364 **IV. ANTICIPATED EFFECTS OF ACACIA INVASION OF RIPARIAN AREAS ON**
365 **STREAMS – A CONCEPTUAL MODEL**

366 **(1) Changes in water quality**

367 Soils in *Acacia* stands generally have higher N concentrations than soils with lower densities
368 of N-fixing species, as a result of N-rich root exudates from *Acacia* trees and decomposition of N-
369 rich litter (Marchante *et al.*, 2008; Lorenzo *et al.*, 2010; Hellmann *et al.*, 2011; González-Muñoz *et*
370 *al.*, 2012; Lazzaro *et al.*, 2014; Souza-Alonso *et al.*, 2014b). Litter from some *Acacia* species,
371 especially those with phyllodes (i.e. leaf-like structures derived from modified petioles, ‘leaves’
372 hereafter; e.g. *A. melanoxylon*, *A. longifolia* and *A. saligna*) decompose slowly, accumulating in a
373 thick layer on the soil surface, and promoting continuous N enrichment of the soil (Marchante *et al.*,
374 2008, 2019; Incerti *et al.*, 2018). The N-rich soil of *Acacia* stands changes the N nutrition of nearby
375 non-N-fixing plants that are able to use fixed atmospheric N (Hoogmoed *et al.*, 2014), which can
376 translate into an increase in their foliar N concentration (Hellmann *et al.*, 2011). Increases in foliar
377 N concentration in non-N-fixing species growing in the presence of N-fixing species seem to be
378 common. A meta-analysis found higher foliar N concentration in non-N-fixing species growing in
379 mixed tree plantations with N-fixing species than in monocultures, while no change in foliar N
380 concentration was found when the mixture did not include N-fixing species (Richards *et al.*, 2010).
381 Also, foliar N concentration was higher in non-N-fixing species when growing under than away
382 from the canopy of N-fixing native *Alnus crispa* in different ecosystems in Alaska (Rhoades *et al.*,
383 2001). N-rich soil leachates and in-stream decomposition of N-rich litter inputs from the riparian
384 vegetation (both *Acacia* litter and litter from native species growing in *Acacia* stands) may
385 contribute to increased N concentrations in streams flowing through *Acacia* stands, as occurs in
386 streams flowing through stands dominated by other N-fixing woody species [native *Alnus* spp.
387 (Compton *et al.*, 2003; Shaftel, King & Back, 2012); invasive species (Goldstein *et al.*, 2009;
388 Atwood *et al.*, 2010; Mineau *et al.*, 2011; Wiegner *et al.*, 2013; Stewart *et al.*, 2019)] (Tables 1, 2;
389 Fig. 4). However, the magnitude of increases in N concentrations in streams will likely depend on

390 the stand density, extent and duration of the invasion as well as on the characteristics of the native
391 and invasive species. For instance, N concentrations in stream water generally increase with
392 increasing cover by N-fixing species at the watershed scale [*Alnus* spp. (Shaftel *et al.*, 2012); *E.*
393 *umbellata* (Goldstein *et al.*, 2009); *U. europaeus* (Stewart *et al.*, 2019)]. When N-fixing species are
394 only in the riparian area, increases in cover affect stream water N concentrations much less or the
395 effects are negligible [*A. rubra* (Compton *et al.*, 2003; Kominoski *et al.*, 2011)].

396 The effects of *Acacia* invasion on dissolved phosphorus (P) concentration are more difficult to
397 anticipate. Increases in N availability in stream water could lead to decreases in P concentration due
398 to increased P uptake by microbes. Indeed, a negative correlation between NO₃-N and dissolved
399 reactive P was found for streams flowing through riparian areas invaded by the N-fixing *U.*
400 *europaeus* (Stewart *et al.*, 2019). However, other studies comparing streams flowing through areas
401 invaded by N-fixing species and non-invaded areas found no significant differences in P
402 concentrations in stream water (Atwood *et al.*, 2010; Mineau *et al.*, 2011; Wiegner *et al.*, 2013).

403

404 **(2) Changes in water quantity**

405 Invasion of deciduous forests by *Acacia* species may decrease stream water availability
406 because these fast-growing evergreen species establish very dense stands, which translates into high
407 transpiration rates with consequent decreases in soil water content (Dye & Jarman, 2004; Le Maitre
408 *et al.*, 2015; Lorenzo & Rodríguez-Echeverría, 2015) (Fig. 4). Water consumption by *A.*
409 *melanoxyton* was estimated as being very high (higher than that of *Eucalyptus globulus* and *Pinus*
410 *pinaster*, which are regarded as having high water demands) in a dense stand in the north-western
411 Iberian Peninsula (Jiménez *et al.*, 2010). In South Africa, water uptake by *Acacia* species (including
412 *A. dealbata* and *A. melanoxyton*) accounted for a substantial portion of the mean annual runoff (Le
413 Maitre, Versfeld & Chapman, 2000). Changes in water uptake and runoff are generally stronger
414 when invasive and native species differ most in structure and deciduousness and where water
415 availability is higher (Le Maitre *et al.*, 2015; Mkunyanana *et al.*, 2019). Thus, potential strong effects

416 on stream water availability are expected when deciduous forests with seasonal dormancy are
417 replaced by evergreen *Acacia* species, especially in riparian areas. The high water demand by
418 *Acacia* species may result in flow intermittency during the warmest and driest periods of the year,
419 which are expected to increase in frequency and duration under a global change scenario,
420 particularly in Mediterranean areas (IPCC, 2013).

421

422 **(3) Changes in litter inputs to streams**

423 *(a) Changes in the diversity of litter inputs*

424 Invasive *Acacia* species have strategies to increase their cover and out-compete native species
425 (Table 5), which frequently leads to the establishment of pure *Acacia* stands (Hellmann *et al.*, 2011;
426 Lorenzo *et al.*, 2012; Marchante *et al.*, 2015). As invasion proceeds, the contribution of *Acacia*
427 species to litter inputs to streams will likely increase. At early stages of invasion this will translate
428 into an increase in the diversity of litter inputs, since there will be a higher number of species in the
429 riparian vegetation (Fig. 4). However, as invasion progresses and native species are replaced by
430 *Acacia* species, the diversity of litter inputs may dramatically decrease and these may become
431 dominated by *Acacia* litter (Fig. 4), which contrasts with litter inputs to streams flowing through
432 more diverse deciduous forests (Lecerf *et al.*, 2005; Swan, Gluth & Horne, 2009; Ferreira *et al.*,
433 2016a).

434

435 *(b) Changes in the phenology of litter inputs*

436 Changes in the timing of litter inputs to streams are also expected with *Acacia* invasions (Fig.
437 4). While in deciduous forests trees shed their leaves mainly in autumn/winter (Abelho & Graça,
438 1996; Molinero & Pozo, 2004), in evergreen *Acacia* stands litter inputs are expected year-round,
439 eventually with a summer peak due to water stress, as observed for other evergreens (e.g. Abelho &
440 Graça, 1996; Molinero & Pozo, 2004) (Table 4). *Acacia* species also shed pods and seeds in
441 summer (Lorenzo *et al.*, 2010), which may contribute to the organic matter input peak in this season

442 (Fig. 5A). Moreover, the accumulation of large amounts of *Acacia* litter on soils as a result of slow
443 decomposition, at least for species with phyllodes (Incerti *et al.*, 2018; Marchante *et al.*, 2019), may
444 lead to high amounts of lateral litter inputs to streams during high rainfall events on steep slopes.

445

446 (c) *Changes in the typology of litter inputs*

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

456

457 (d) *Changes in the quantity of litter inputs*

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

464

465 (e) *Changes in the quality of litter inputs*

466 Physical (e.g. toughness) and chemical (e.g. concentrations of nutrients and structural and
467 secondary compounds) characteristics differ among leaf species and organic matter types (e.g.

468 leaves, flowers, fruits, wood) (Molinero & Pozo, 2006; Castro-Díez *et al.*, 2012; Table 4). Thus,
469 changes in diversity, typology and quantity of litter inputs to streams in *Acacia* stands will likely be
470 accompanied by changes in nutrient inputs (Fig. 4). The direction and magnitude of these changes
471 will also depend on the species composition of the invaded systems. If a deciduous forest dominated
472 by species such as *C. sativa* and *Quercus* spp. is invaded by *A. dealbata*, there will likely be an
473 increase in litter N inputs to streams, as the invasive species is richer in N than the natives (Castro-
474 Díez *et al.*, 2012). Changes are expected even when *A. dealbata* invades riparian areas dominated
475 by native N-fixing species, such as *Alnus glutinosa*, resulting from differences in litter input
476 phenology, typology and quantity.

477

478 (f) Changes in allelopathic compounds

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

493 assume that leachates released from *Acacia* litter after immersion in streams may inhibit litter
494 colonization by microbes and litter decomposition (Fig. 4).

495
496 **(4) Changes in stream litter decomposition and aquatic communities**

497 *(a) Response to changes in water quality*

498 Litter decomposition is a fundamental process in forest streams, allowing the incorporation of
499 litter carbon and nutrients into the aquatic food web thus promoting nutrient cycling (Wallace *et al.*,
500 1997; Marks, 2019). Litter decomposition is mostly a biological process, carried out by microbial
501 decomposers, mainly aquatic hyphomycetes, and benthic invertebrates, mainly shredders (Gessner
502 *et al.*, 2010; Marks, 2019), which are sensitive to environmental changes. Moderate increases in
503 dissolved N availability stimulate microbial activity [e.g. reproduction, growth and metabolism
504 (Gulis & Suberkropp, 2003; Gulis, Ferreira & Graça, 2006)], invertebrate colonization of litter [e.g.
505 taxa richness, abundance and biomass (Gulis *et al.*, 2006; Greenwood *et al.*, 2007)] and
506 consequently litter decomposition in streams (Woodward *et al.*, 2012; Ferreira *et al.*, 2015a;
507 Rosemond *et al.*, 2015). Expected increases in dissolved N availability in streams flowing through
508 *Acacia* stands may thus stimulate microbial activity, invertebrate colonization and ultimately litter
509 decomposition (Fig. 4).

510 Effects of increases in N concentration in stream water may, however, depend on background
511 N and P concentrations. When background N concentrations are not limiting, moderate increases in
512 N concentrations may not have noticeable effects on aquatic communities or litter decomposition
513 (Chadwick & Huryn, 2003; Baldy *et al.*, 2007). Thus, effects of nutrient enrichment tend to be
514 lower when background nutrient concentrations are higher (Ferreira *et al.*, 2015a). Also, when
515 background P concentrations are limiting, increases in N concentrations may not have noticeable
516 effects on litter decomposition (Ferreira *et al.*, 2015a). Additionally, effects of N enrichment may
517 be stronger for larger N increases (Ferreira *et al.*, 2015a), which may relate to the extent and
518 duration of the invasion.

519 The impact of increases in stream water N availability on decomposer activity and litter
520 decomposition may also depend on litter characteristics. Nutrient effects on microbial activity and
521 litter decomposition are generally stronger for nutrient-poor than for nutrient-rich litter, where
522 microbial activity is generally not nutrient limited (Gulis & Suberkropp, 2003; Ferreira, Gulis &
523 Graça, 2006b; Gulis *et al.*, 2006; Kominoski *et al.*, 2015). Moreover, nutrient effects are generally
524 stronger for lignin-poor than for lignin-rich litter, where microbial activity may be carbon (C)
525 limited since lignin is highly refractory and also limits microbial access to labile C sources (Jabiol
526 *et al.*, 2019).

527 Therefore, changes in microbial activity and litter decomposition in streams in *Acacia* stands
528 will finally depend on the interaction between increases in dissolved N availability and litter
529 characteristics. *Acacia* leaves are N-rich, but N accessibility to microbes may depend on leaf
530 toughness and lignin concentration. For instance, *A. melanoxylon* leaf litter is tough and has high
531 lignin concentration (low C quality). Consequently, litter decomposition is slow and may be less
532 sensitive to dissolved nutrient concentration than that of litter with higher C quality (Ferreira *et al.*,
533 2016b).

534 Woody materials are abundant in *Acacia*-dominated streams (Fig. 5B). They have high C to N
535 ratios and are sensitive to increases in dissolved nutrient concentrations (Gulis *et al.*, 2004; Gulis,
536 Suberkropp & Rosemond, 2008; Ferreira *et al.*, 2006b). Recalcitrant litter (e.g. tough leaves and
537 woody material) is, however, colonized slowly, sustains lower microbial activity and is decomposed
538 at a lower rate than high-quality litter (i.e. soft, with high nutrient concentrations and low
539 concentrations of secondary and structural compounds) (Ferreira *et al.*, 2006b; Gulis *et al.*, 2008).
540 Thus, despite possible stimulation of litter decomposition by increases in dissolved N availability in
541 streams flowing through *Acacia* stands, if these streams receive higher proportions of recalcitrant
542 litter compared with streams in deciduous forests, the absolute rate of litter decomposition may still
543 be lower in the invaded than in the native streams. A reduction in overall litter decomposition may
544 impair nutrient cycling through the food web (Hladyz *et al.*, 2011).

545 Additionally, the impact of nutrient enrichment on litter decomposition may depend on the
546 presence of shredders. Feeding activities of shredders on leaves are stimulated by litter microbial
547 conditioning (Bärlocher & Sridhar, 2014), which is promoted by increases in water nutrient
548 concentration (Gulis & Suberkropp, 2003; Gulis *et al.*, 2006). Thus, when shredders are present,
549 they may amplify the stimulatory effect that nutrient enrichment has on microbial communities
550 (Gulis *et al.*, 2006). On the contrary, if shredder abundance decreases in streams in *Acacia* stands as
551 a result of stream flow intermittency or litter recalcitrance (see Section IV.4b, IV.4c), effects of
552 nutrient enrichment on litter decomposition may be limited.

553

554 *(b) Response to changes in water quantity*

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

567

568 *(c) Response to changes in litter input characteristics*

569 Increases in *Acacia* species cover and changes in litter input characteristics may also affect
570 aquatic communities, especially those involved in the detrital pathway, which strongly depend on

571 litter inputs for food and substrate (Wallace *et al.*, 1997; Gessner *et al.*, 2010) (Fig. 4). Species
572 richness of aquatic hyphomycetes and benthic macroinvertebrates is generally positively correlated
573 with species richness of riparian trees and benthic litter (Laitung & Chauvet, 2005; Lecerf *et al.*,
574 2005; Ferreira *et al.*, 2016a). A decrease in riparian tree diversity in *Acacia* stands may thus lead to
575 decreases in aquatic biological diversity and abundance, as shown for the replacement of deciduous
576 forests by *E. globulus* monocultures (Bärlocher & Graça, 2002; Ferreira *et al.*, 2006a, 2015b;
577 Larrañaga, Basaguren & Pozo, 2009). Lowe *et al.* (2008) also found lower abundances of cobble-
578 dwelling taxa and higher abundances of particle-feeding mayflies and chironomids in streams
579 flowing through areas invaded by *A. mearnsii* than in streams flowing through native Fynbos
580 vegetation in South Africa. Decreases in the diversity, abundance and biomass of
581 macroinvertebrates (shredders in particular) generally lead to decreases in litter decomposition
582 (Piscart *et al.*, 2009; Ferreira *et al.*, 2016a; Monroy *et al.*, 2016).

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

591 Changes in litter decomposition rates in streams in *Acacia* stands, and consequently in
592 nutrient cycling, are therefore difficult to anticipate since they depend primarily on how stream
593 water quality and quantity, litter inputs and aquatic communities will change in response to the
594 *Acacia* invasion of deciduous forests. However, if the changes discussed above are confirmed (Fig.
595 4), *Acacia* species may well act as transformers (ecosystem engineers) of aquatic ecosystems as
596 they do for terrestrial ecosystems (Richardson & Rejmánek, 2011).

597 Effects of *Acacia* invasions on soil detrital pathways have been documented (Ehrenfeld, 2003;
598 Souza-Alonso *et al.*, 2017). For instance, the invasion of South African grasslands by *A. dealbata*
599 led to decreases in dung coleopteran species richness, abundance and body size, with consequent
600 changes in community composition (Coetzee, Rensburg & Robertson, 2007). Invasion by *A.*
601 *melanoxydon* and *A. mearnsii* in South Africa led to decreases in soil invertebrate species richness,
602 but not family richness, suggesting that changes in species richness may not be translated into
603 functional changes (Samways, Caldwell & Osborn, 1996). The effects of *Acacia* invasion on soil
604 invertebrates may be mediated by detrimental effects on species ecology. Sousa *et al.* (1998) found
605 lower growth rates and growth efficiencies of the isopod *Porcellio dilatatus* when fed with *A.*
606 *longifolia* than with native *Alnus glutinosa* or *Quercus* sp. leaves, despite the higher consumption of
607 *A. longifolia* litter (likely due to compensatory feeding).

608

609 **V. CONCEPTUAL FRAMEWORK TO PREDICT EFFECTS OF INVASION OF** 610 **RIPARIAN AREAS BY N-FIXING SPECIES ON STREAMS**

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

623 (assuming strong similarities with *Salix cinerea*) compared to *A. glutinosa* (Kučerová *et al.*, 2001),
624 discharge is expected to be lower in streams flowing through forests with low than high
625 representation of N-fixing species (Fig. 6D). Owing to the lower water N concentration and lower
626 nutritional quality of the litter input (e.g. lower litter N concentration) in streams flowing through
627 forests with low cover of N-fixing species, litter decomposition potential (i.e. overall decomposition
628 of benthic organic matter) is expected to be lower in these streams compared with streams flowing
629 through forests dominated by N-fixing species that have higher water N concentration and receive
630 soft, N-rich *A. glutinosa* litter (Fig. 6E, F).

631 During invasion by *Acacia* species, riparian tree species richness first increases, while at
632 advanced stages of invasion it decreases as the riparian vegetation becomes a (nearly) monospecific
633 *Acacia* stand (Section III.2; Table 5; Fig. 6A). During invasion, cover by N-fixing species also
634 increases as the cover by *Acacia* species increases (Fig. 6B). Consequently, water N concentration
635 increases (Fig. 6C) through the pathways described above (Section IV.1; Fig. 4). Stream discharge
636 decreases (Fig. 6D) as the evergreen, fast-growing *Acacia* form dense stands, translating into
637 increased evapotranspiration (Section IV.2; Fig. 4). Litter decomposition potential increases with
638 increases in water N concentration and litter input diversity at early stages of invasion (Fig. 6E, 6F),
639 as decomposer activity is promoted by increased nutrient availability (‘productivity hypothesis’)
640 and substrate diversity (‘niche complementarity hypothesis’) (Ferreira *et al.*, 2016a; Sections IV.4a,
641 IV.4c; Fig. 4). At advanced stages of invasion, litter decomposition potential can increase further
642 (Fig. 6E), if effects mediated by increased water N concentrations prevail (Section IV.4a; Fig. 4), or
643 it can decrease (Fig. 6F), if effects mediated by increases in litter recalcitrance (e.g. increases in
644 wood inputs) prevail when the riparian vegetation is dominated by *Acacia* (Section IV.4a; Fig. 4).
645 When invasion promotes streambed drying, litter decomposition can be further reduced (Section
646 IV.4b). The effects of invasion on stream processes will depend on the interactions of multiple
647 pathways and are therefore more difficult to predict compared with changes in environmental
648 variables. At early stages of *Acacia* invasion, effects are small and differences between forests with

649 low and high representation of N-fixing species are maintained compared with the pre-invasion
650 condition. At advanced stages of invasion, however, effects become stronger and similar for both
651 forest types as the riparian vegetation becomes a monospecific *Acacia* stand (Fig. 6). Although the
652 final effects of *Acacia* invasion may be similar for riparian forests with low or high representation
653 of N-fixing species, the magnitude of the effects will differ given the initial differences between
654 forest types (Fig. 6).

655

656 VI. DECOMPOSITION OF ACACIA LEAF LITTER IN STREAMS

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

664 Reported decomposition rates (k , day⁻¹) for *Acacia* leaf litter vary from slow ($k < 0.005$) to
665 medium ($0.005 < k < 0.010$) to fast ($k > 0.010$) [using Petersen & Cummins (1974) categories of
666 decomposition rates], both within and across species (Table 6). However, comparisons among
667 species, or even within species, are limited by differences in the type of *Acacia* leaves,
668 methodologies, and incubation conditions. Still, it seems that litter decomposition (at least for *A.*
669 *longifolia* and *A. melanoxylon*, which have phyllodes) is mostly microbial-driven (Table 6). Also,
670 litter decomposition rates are sensitive to environmental conditions (e.g. Campbell *et al.*, 1992;
671 Serra & Abelho, 2018; Table 6). The only study that compared *Acacia* (*A. mearnsii*, with ‘true’
672 leaves) litter decomposition in streams flowing through *Acacia* stands and native vegetation
673 (Fynbos) found no significant differences between stream types, although decomposition was faster
674 for *A. mearnsii* than for Fynbos species (Railoun, 2018). These latter results contrast with our

675 proposed model (Figs 4, 6), but we need to bear in mind that Fynbos vegetation is dominated by
676 evergreen sclerophyllous plants, which likely produce recalcitrant litter that decomposes more
677 slowly than that of *A. mearnsii*. This highlights the need to consider differences in the
678 invaded/invasive system when comparing results across studies and extrapolating the conceptual
679 model to other systems.

680

681 **VII. IMPACTS OF INVASIVE N-FIXING SPECIES ON ECOSYSTEM SERVICES**

682 **PROVIDED BY STREAMS**

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

693 Many stream processes are important not only locally but also downstream; for instance, litter
694 decomposition releases dissolved nutrients and fine particulate organic matter that can be
695 incorporated into food webs downstream (MacDonald & Coe, 2007; Wipfli, Richardson & Naiman,
696 2007). Additionally, stream processes are important to the riparian ecosystem; for instance, aerial
697 stages of aquatic insects can be food for riparian predators (Nakano & Murakami, 2001; Chika,
698 Iwata & Eitaro, 2004; Baxter, Fausch & Saunders, 2005). Thus, local changes to stream ecosystem
699 functioning may have far-reaching consequences. The potential for strong effects of invasive N-

700 fixing species on stream functioning, and consequently on ecosystem services, make management
701 of invasions in riparian forests a priority.

702

703 **VIII. FUTURE DIRECTIONS**

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

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

724 Effects of invasions should be assessed on multiple stream components (i.e. sediments, water,
725 organic matter, communities and processes) and ideally include the stream–riparian forest meta-

726 ecosystem. Importantly, effects of invasion by N-fixing species on the multiple components of
727 stream ecosystems need serious attention as these may influence multiple ecosystem services (Table
728 7). Determining the pathways of action (e.g. *via* changes in water quality, water quantity, quantity
729 and quality of litter inputs) will be useful for the establishment of mitigation measures.

730

731 **IX. CONCLUSIONS**

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

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

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

747 (4) The multiple effects of tree invasion on streams may jeopardize the services that these
748 ecosystems provide to human populations, which is of great concern given the small area occupied
749 by streams worldwide and the strong dependency of humans on their services (e.g. good quality
750 water).

751 (5) Given the potential effects of N-fixing tree invasion on stream ecosystem services, it is
752 surprising how little research there is on this topic compared with that addressing the effects of
753 other environmental changes. The proposed model helps to anticipate effects of forest invasion by
754 N-fixing trees on streams, but the magnitude of these effects still remains to be quantified. Research
755 on the effects of forest invasion on streams should be a priority as is the case for other human-
756 induced environmental changes (e.g. emerging contaminants), allowing better management of
757 stream–riparian forest meta-ecosystems.

758

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766

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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.

Invasive species	Native region	Study region and native vegetation	Stream characteristic	Effects of the invasion (response in invaded compared with non-invaded condition)	Reference
<i>Acacia mearnsii</i> (black wattle)	Australia	Cape Floristic Region, South Africa; Fynbos shrubland	Benthic macroinvertebrates	Lower abundance of cobble-dwelling taxa; higher abundance of particle-feeding mayflies and chironomids	Lowe <i>et al.</i> (2008)
			Litter fall dynamics (~ litter input dynamics)	Higher annual amount of litter fall; change in phenology of litter fall; higher N concentration in leaf litter	Railoun (2018)
			Decomposition of native and <i>A. mearnsii</i> leaf litter in fine mesh bags	No effect of invasion; faster decomposition of <i>A. mearnsii</i> than native litter	Railoun (2018)
			Macroinvertebrate density associated with native and <i>A. mearnsii</i> leaf litter decomposing in coarse mesh bags	No effect of invasion or litter type	Railoun (2018)
			Sediment-associated nutrients	Higher total C and total P concentrations in sediments (but context dependent)	Wiener <i>et al.</i> (2020)
<i>Elaeagnus angustifolia</i> (Russian olive)	Western and Central Asia	Western USA; sagebrush steppe	Stream water quality	Higher organic N concentration	Mineau <i>et al.</i> (2011)
			Nutrient limitation of biofilms	Lower N limitation	Mineau <i>et al.</i> (2011)
			Ammonium (NH ₄ -N), nitrate (NO ₃ -N) and phosphate (PO ₄ -P) uptake	Higher demand for NH ₄ -H and NO ₃ -N at inorganic N low background concentrations	Mineau <i>et al.</i> (2011)
			Litter fall (~ litter input)	Higher amount of litter fall	Mineau <i>et al.</i> (2012)
			Leaf litter decomposition	No effect of invasion; faster decomposition of <i>E. angustifolia</i> than native <i>Salix amygdaloides</i> litter	Mineau <i>et al.</i> (2012)

			Instream primary production	No change despite reduction in canopy cover	Mineau <i>et al.</i> (2012)
			Benthic organic matter	Higher storage; no changes in ecosystem respiration; no change in organic matter export	Mineau <i>et al.</i> (2012)
			Stream ecosystem efficiency	Lower respiration/organic matter input ratio	Mineau <i>et al.</i> (2012)
<i>Elaeagnus umbellata</i> (autumn-olive)	Eastern Asia	Eastern USA; deciduous broadleaf forest	Stream water quality	Positive correlation between NO ₃ -N and <i>E. umbellata</i> cover	Goldstein <i>et al.</i> (2009)
<i>Falcataria moluccana</i> (albizia)	Maluku Islands, New Guinea Island, Bismarck Archipelago and Solomon Islands	Hawaii; lowland wet forest	Stream water quality	Higher NO ₃ +NO ₂ concentration	Atwood <i>et al.</i> (2010)
			Food-web structure	<i>F. moluccana</i> became a major contributor to diets of lower-level consumers, displacing particulate organic matter and macroalgae; <i>F. moluccana</i> likely is an important N source for benthic primary producers	Atwood <i>et al.</i> (2010)
			Stream water quality	Higher NO ₃ +NO ₂ concentration; lower organic N and organic C concentrations	Wiegner <i>et al.</i> (2013)
			Nutrient limitation of biofilms	Higher benthic chlorophyll- <i>a</i> ; lower N limitation	Wiegner <i>et al.</i> (2013)
<i>Ulex europaeus</i> (European gorse)	British Isles and Western Europe	Banks Peninsula, New Zealand; podocarp forest	Stream water quality	Higher NO ₃ concentration due to decomposition of <i>U. europaeus</i> litter; positive correlation between NO ₃ concentration and <i>U. europaeus</i> cover for streams where it was present	Stewart <i>et al.</i> (2019)
			N cycle	Lower efficiency in NO ₃ attenuation	Stewart <i>et al.</i> (2019)

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.

Stream characteristic	Effects of the invasion (response in invaded compared with non-invaded condition)	Reference
Stream N concentrations	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	Compton <i>et al.</i> (2003)
	Higher nitrate and total N concentrations	Volk <i>et al.</i> (2003)
	No effect of invasion on N concentrations	Kominoski <i>et al.</i> (2011)
Annual N export	Positive relationship with broadleaf and mixed broadleaf–conifer cover	Compton <i>et al.</i> (2003)
Stream discharge	Potentially lower given the higher transpiration in riparian forests invaded by <i>A. rubra</i> that constitute young-aged stands compared with old-growth conifer forests	Moore <i>et al.</i> (2004)
Litter inputs to streams	Higher annual litter inputs; higher N concentration in litter inputs; higher litter N fluxes to streams	Hart (2006); Volk <i>et al.</i> (2003); Kominoski <i>et al.</i> (2011)
Detritus export	Higher detritus export; positive relationship with percentage canopy cover by <i>A. rubra</i>	Piccolo & Wipfli (2002); Wipfli & Musslewhite (2004)
Periphyton	Higher periphyton biomass	Volk <i>et al.</i> (2003)
	No effect of invasion on chlorophyll- <i>a</i>	Volk <i>et al.</i> (2008)
Microbes associated with decomposing litter	Higher microbial respiration rates in deciduous than in conifer streams for <i>A. rubra</i> leaves; higher respiration rates in mixed deciduous–conifer than conifer streams for <i>Tsuga heterophylla</i> 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 <i>T. heterophylla</i> than <i>A. rubra</i> litter	Kominoski <i>et al.</i> (2011)
Macroinvertebrates associated with decomposing leaves	Higher biomass and abundance in <i>A. rubra</i> leaves than <i>T. heterophylla</i> needles, and higher in mixed <i>A. rubra</i> –conifer than conifer streams; no effect of invasion or litter species on taxon richness; higher taxa evenness in <i>T. heterophylla</i> than <i>A. rubra</i> litter and in conifer streams; effects of invasion and litter species on community structure	Kominoski <i>et al.</i> (2011)
Macroinvertebrates associated with decomposing wood	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	Kimbrauskas <i>et al.</i> (2008)
Macroinvertebrate export	Higher export (number and biomass); positive relationship with percentage canopy cover by <i>A. rubra</i>	Piccolo & Wipfli (2002), Wipfli & Musslewhite (2004)
Litter decomposition	Positive relationship between total decomposition rates of <i>A.</i>	Kominoski <i>et al.</i> (2011)

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.

Country/Region	<i>Acacia dealbata</i>	<i>Acacia melanoxylon</i>	References
North America	X	X	Rejmánek & Richardson (2013)
USA	X	X	Swearingen & Bargeron (2016); Randall (2017); CABI (2019)
Central America		X	Rejmánek & Richardson (2013)
Mexico		X	CONABIO (2018)
South America	X	X	Rejmánek & Richardson (2013)
Argentina	X	X	Zalba & Villamil (2002); Fonseca <i>et al.</i> (2013)
Brazil		X	Fonseca <i>et al.</i> (2013)
Chile*	X	X	Fuentes <i>et al.</i> (2010); Fuentes-Ramírez <i>et al.</i> (2011); CABI (2019)
Colombia		X	Randall (2017)
Uruguay	X		Masciadri <i>et al.</i> (2010)
Atlantic Islands		X	Rejmánek & Richardson (2013)
Europe	X	X	Rejmánek & Richardson (2013)
Algeria	X	X	CABI (2019)
France	X	X	Lorenzo <i>et al.</i> (2010); Ducatillion <i>et al.</i> (2015)
Italy	X		Celesti-Grapow <i>et al.</i> (2009); Lorenzo <i>et al.</i> (2010)
Portugal*	X	X	Marchante <i>et al.</i> (2014)
Spain*	X	X	Sanz-Elorza <i>et al.</i> (2004); Lorenzo <i>et al.</i> (2010)
Switzerland	X		Schoenenberger <i>et al.</i> (2014)
Turkey	X		Atasoy & Çorbacı (2018)
Africa (southern)	X	X	Rejmánek & Richardson (2013)
Lesotho		X	Witt & Luke (2017)
South Africa*	X	X	Henderson (1992); van Wilgen & Wilson (2018)
Swaziland	X	X	Swaziland National Trust Commission (2019)
Zimbabwe		X	Maroyi (2012); Witt & Luke (2017); CABI (2019)
Africa (central)		X	Rejmánek & Richardson (2013)
Congo	X	X	Mbale (2010); Randall (2017)
Ethiopia		X	Randall (2017)
Kenya		X	Witt & Luke (2017)
Tanzania		X	CABI (2019)
Asia		X	Rejmánek & Richardson (2013)
Bhutan		X	Sankaran & Suresh (2013)

China	X	X	Axmacher & Sang (2013); Sankaran & Suresh (2013)
India	X	X	Sankaran & Suresh (2013); Sekar (2015); Randall (2017); CABI (2019)
Israel	X	X	Dufour-Dror (2013)
Pakistan		X	Witt & Luke (2017)
Sri Lanka	X	X	Sankaran & Suresh (2013); CABI (2019)
Thailand		X	Sankaran & Suresh (2013)
Indian Ocean Islands	X		Rejmánek & Richardson (2013)
Madagascar	X		Binggeli (2003)
Reunion Island	X		Tassin <i>et al.</i> (2006)
Australia	X	X	Rejmánek & Richardson (2013)
Pacific Islands		X	Rejmánek & Richardson (2013)
Hawaii		X	CABI (2019)
Japan		X	Sankaran & Suresh (2013)
New Caledonia		X	Sankaran & Suresh (2013)
New Zealand*	X	X	Howell (2008); CABI (2019)
Taiwan	X		EFlora.org (2015)

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).

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

	phenology								
N-fixer	N-fixing trees may increase water nutrient concentration and N concentration of litter fall	Yes	Yes	No	No	No	No	No	Yes
Growth rate	Fast growth rates may lead to the fast production of high amounts of litter	Fast	Fast	Slow	Slow	Fast	Fast	Fast	Fast
Longevity	Long life forms are more efficient in stabilizing stream margins	Short (30–40 years)	Long (max. > 200 years)	Very long (max. 500–600 years, exceptionally > 1000 years)	Very long (max. > 1000 years)	Not very long (max. 70 years)	Long (max. 200–300 years)	Long (max. 200 years)	Not very long (max. 100–120 years)
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	Extensive and superficial	Tolerates flooding	Strong and deep with pivoting main root and extensive secondary roots; prefers fertile and well-watered soils; mature trees tolerate 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 and large leaves are better retained in the stream reach	Bipinnate leaf with large number of very small leaflets	Entire small-sized leaf (phyllode)	Entire medium–large-sized leaf	Entire large-sized leaf	Entire small-sized leaf	Entire medium-sized leaf	Pinnate large-sized leaf with small number of leaflets	Entire medium-sized leaf
Leaf litter quality	Soft and nutrient-rich leaf litter is colonized and decomposed faster than more recalcitrant leaf litter; recalcitrant leaf litter sustains	Low lignin:N	Tough; low lignin:N	Tough; high lignin:N; high condensed tannins	High lignin:N	High lignin:N; high polyphenol concentrations	High lignin:N; high polyphenol concentrations	Low lignin:N	Soft; low lignin:N; low condensed tannins

	aquatic food webs later in the year after it has been conditioned by microbial decomposers								
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.

Characteristics	Consequences	Key references
Establish symbiotic relationships with N-fixing bacteria	Ability to colonize and establish in low-quality soils, which potentially alters soil and stream water characteristics	Le Roux <i>et al.</i> (2018)
High adaptability to different environmental conditions and to environmental change	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	Lorenzo <i>et al.</i> (2010)
Production of large numbers of resistant seeds with easy germination that can accumulate in the soil for long periods	Rapid establishment of pure <i>Acacia</i> 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	Richardson & Kluge (2008)
Production of allelopathic compounds that inhibit the germination of seeds from other species		Souza-Alonso <i>et al.</i> (2014a)
High growth rates and the capacity to accumulate high biomass		Le Maitre <i>et al.</i> (2011)
Resprout after cutting, fire or frost		Richardson <i>et al.</i> (2011)

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 & Middleton (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.

Acacia species	k (day⁻¹)	Incubation conditions and location	Reference
<i>Acacia auriculiformis</i> (earleaf acacia)*	0.0063–0.0081	Air-dried senescent litter in coarse mesh bags; streams in the Western Ghat forest (India)	Raviraja <i>et al.</i> (1996)
<i>Acacia longifolia</i> (long-leaved wattle)*	0.52 % loss/d	Air-dried litter in coarse-mesh bags; stream in central Anatolia (Turkey)	Akanil & Middleton (1997)
	0.0083–0.0195	Litter in coarse-mesh bags; peri-urban stream reaches in central Portugal	Serra & Abelho (2018)
	0.008	Litter in coarse-mesh bags; peri-urban stream in central Portugal	Couceiro & Abelho (2015)
	0.008	Litter in fine-mesh bags; peri-urban stream in central Portugal	Couceiro & Abelho (2015)
<i>Acacia mearnsii</i> (black wattle)	0.0225–0.0241	Oven-dried (50°C) senescent litter in fine-mesh bags; near-pristine streams in the Cape Floristic Region (South Africa)	Railoun (2018)
	0.0216–0.0277	Oven-dried (50°C) senescent litter in fine-mesh bags; invaded streams in the Cape Floristic Region (South Africa)	Railoun (2018)
<i>Acacia melanoxylon</i> (Australian blackwood)*	0.0040–0.0073	Leached and oven-dried (40 °C) senescent litter in coarse mesh bags; stream reaches in south-eastern Australia (native range)	O'Keefe & Lake (1987)
	0.0026–0.0084	Air-dried senescent litter in packs; streams in south-eastern Australia (native range)	Campbell <i>et al.</i> (1992)
	0.0037–0.0415	Air-dried fresh litter in packs; streams in south-eastern Australia (native range)	Campbell <i>et al.</i> (1992)
	0.008–0.011	Air-dried senescent litter in coarse-mesh bags; insular streams (Azores)	Raposeiro <i>et al.</i> (2014)
	0.006–0.007	Air-dried senescent litter in fine-mesh bags; insular streams (Azores)	Raposeiro <i>et al.</i> (2014)
	0.0068–0.0106	Air-dried fresh litter in coarse-mesh bags; insular streams over a gradient of dissolved nutrients	Ferreira <i>et al.</i> (2016b)

	(Azores)	
0.0064–0.0102	Air-dried fresh litter in fine-mesh bags; insular streams over a gradient of dissolved nutrients (Azores)	Ferreira <i>et al.</i> (2016b)
0.0047	Air-dried fresh litter in coarse-mesh bags; insular stream (Azores)	Raposeiro <i>et al.</i> (2018)
0.0053	Air-dried fresh litter in fine-mesh bags; insular stream (Azores)	Raposeiro <i>et al.</i> (2018)

Table 7. Stream ecosystem services that may be affected by the invasion of temperate deciduous forests by *Acacia* species. Δ denotes change (with magnitude and direction depending on effects of *Acacia* invasion) and \downarrow denotes decrease.

Type of ecosystem service	Ecosystem service potentially affected by <i>Acacia</i> invasion (direction of change)	Cause of change in ecosystem services resulting from <i>Acacia</i> invasion
Provisioning (supply of goods or services)	Good quality water (\downarrow)	Decrease in water quantity and quality
	Energy production (\downarrow)	Decrease in water quantity
	Food production (e.g. fish) (Δ)	Changes in productivity resulting from changes in food webs and processes
	Biodiversity (e.g. genetic resources) (\downarrow)	Decrease in diversity of litter inputs and environmental conditions
Regulating (non-material benefits)	Litter decomposition and nutrient cycling (Δ)	Changes in water quantity and quality, in litter inputs and in aquatic communities
	Habitat maintenance (Δ)	Input of large amounts of woody material
	Water purification (\downarrow)	Decrease in water quality
	Erosion control (\downarrow)	<i>Acacia</i> tree fall and increase in sediment load
	Climate regulation (Δ)	Increase in transpiration due to dense stands of fast-growing, evergreen <i>Acacia</i> trees; changes in litter decomposition and CO ₂ evasion from streams
	Carbon and nitrogen sequestration (Δ)	Changes in litter decomposition and in incorporation of carbon and nitrogen into food webs due to changes in water quality and litter characteristics
Supporting (services needed to support other services)	Biodiversity (\downarrow)	Decrease in diversity of litter inputs and environmental conditions
	Nutrient cycling (Δ)	Changes in litter decomposition
Cultural and life-enhancing	Aesthetic enjoyment (Δ)	Loss of autumnal colours from native vegetation and effusive blooming of <i>Acacia</i> flowers in late winter
	Recreation: swimming pools (\downarrow)	Decrease in water quantity
	Recreation: fishing (Δ)	Changes in productivity
	Recreation: biodiversity (\downarrow)	Decrease in diversity of litter inputs and environmental conditions
	Science and education (Δ)	Changes in vegetation context with all associated changes

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).

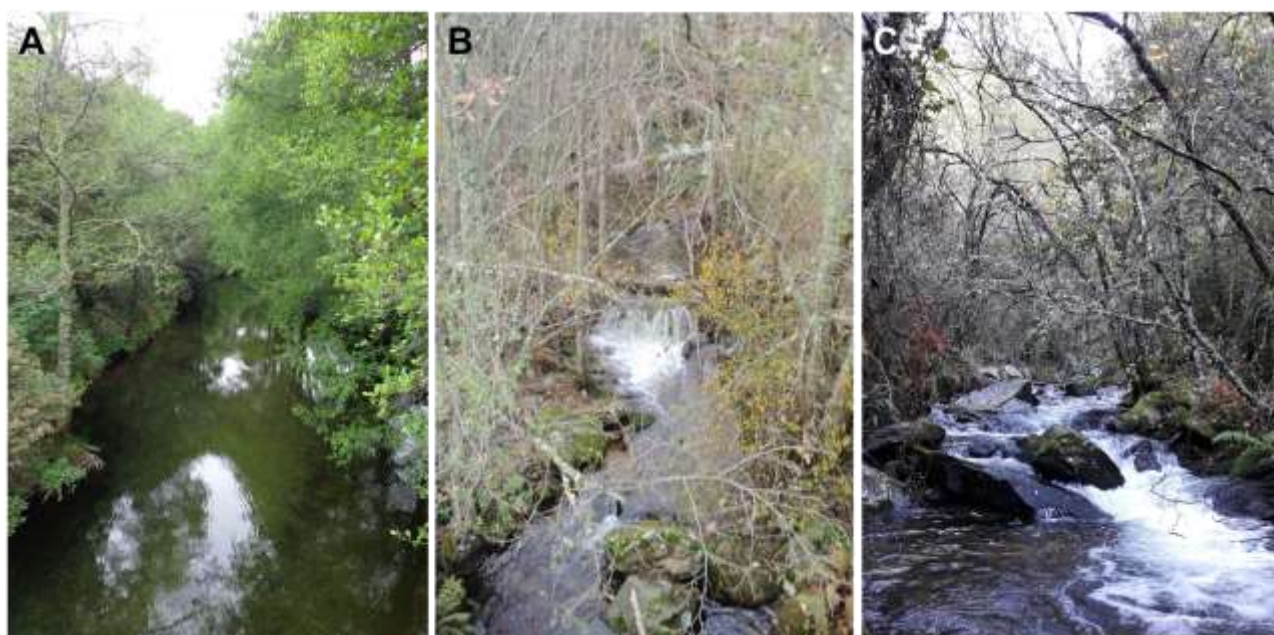


Fig. 2. The extent of the invasion by *Acacia dealbata* in Lousã Mountain, central Portugal, is particularly evident between January and March when the bright yellow flowers are visible (A, B). Often, *Acacia* trees are present on the stream banks where they replace the native riparian vegetation as illustrated for São João stream, Lousã Mountain (C). Photographs taken in February 2017 (©Andreia Ferreira).

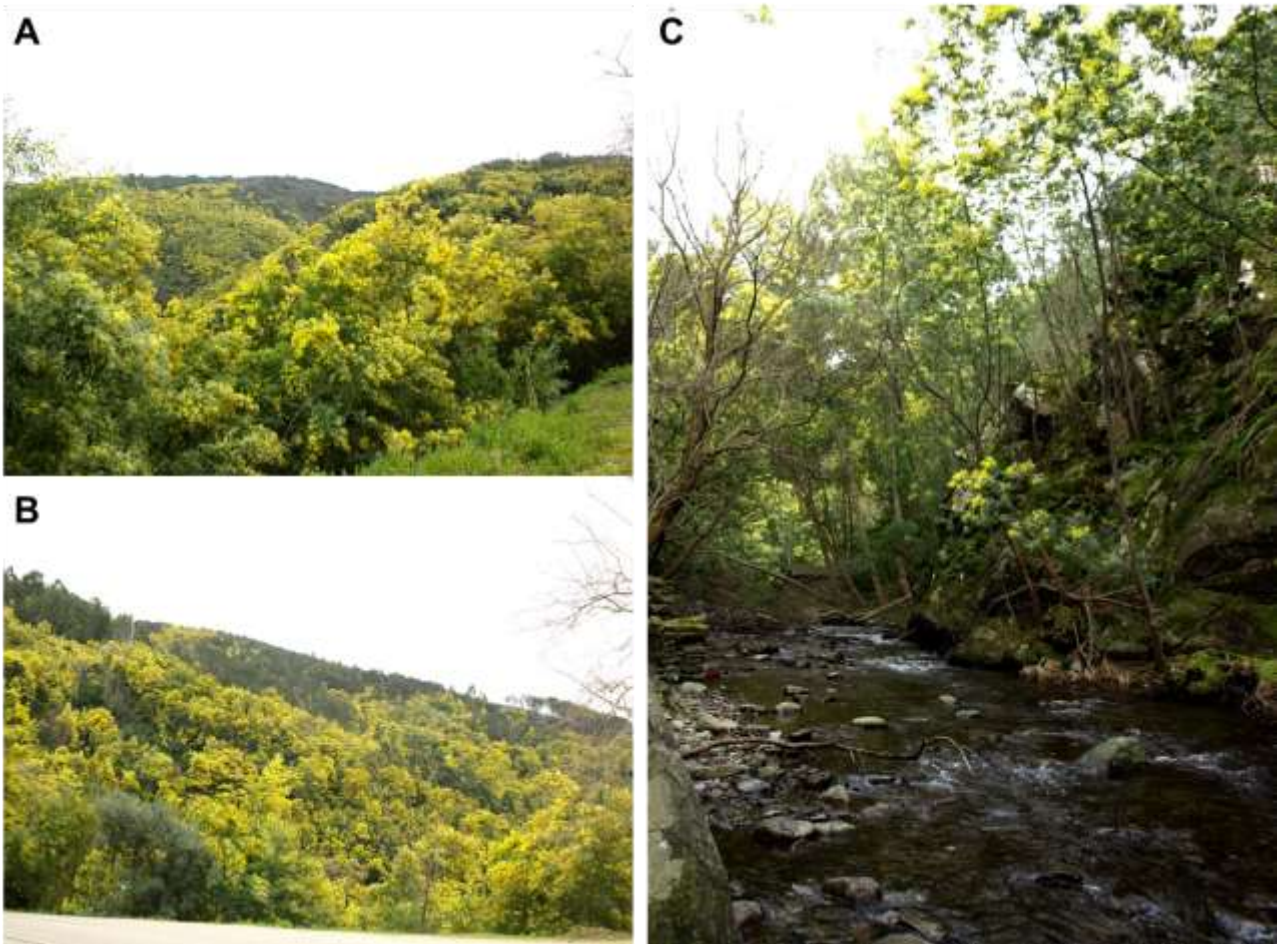


Fig. 3. *Acacia* invasion in the Ceira river watershed, central Portugal. Data sources: presence of *Acacia* species in 1977: Atlas do Ambiente, Carta de Distribuição de acácias e eucaliptos (Comissão Nacional do Ambiente, 1978); area affected by fire in 2017: Institute of Nature Conservation and Forests (ICNF; <http://www2.icnf.pt/portal/florestas/dfci/inc/mapas>, accessed in February 2020); *Acacia* patches in 2018: patch size evaluation based on photointerpretation from Portugal Orthos (ITAP/ICNF funded by Permanent Forest Fund (FFP), 3/1/2018) available from Basemap – ArcMap (ESRI – Environmental Systems Research, accessed in February 2020).

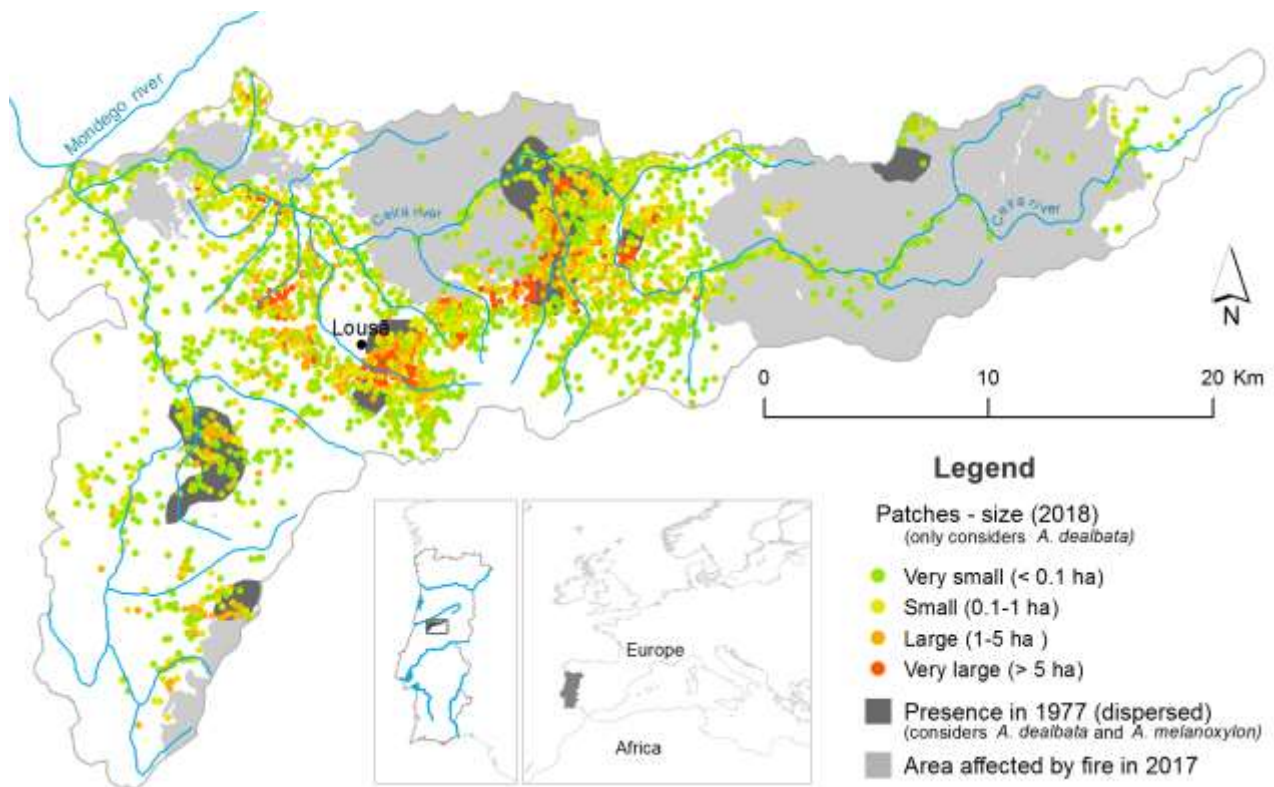


Fig. 4. Conceptual model of possible effects of the invasion of temperate deciduous broadleaf forests by N-fixing species on stream communities and processes. Δ denotes change, \uparrow denotes increase, \downarrow denotes decrease and ? denotes unknown direction of the expected effects.

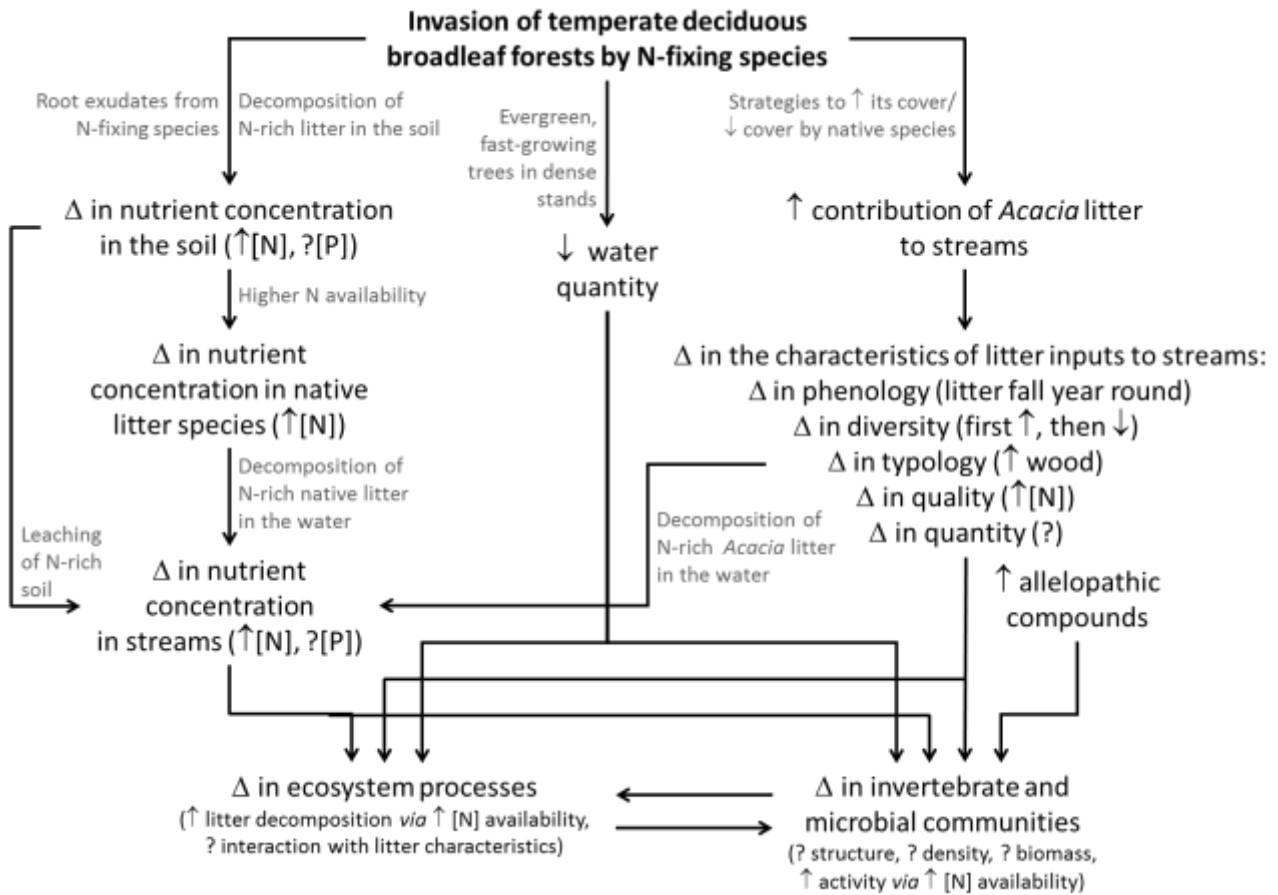


Fig. 5. The contribution of *Acacia* pods (the reddish litter on the forest floor and collecting net) to litter inputs to streams flowing through *Acacia* stands is high during summer (A), and these streams also accumulate large amounts of woody material (B) as illustrated for Sotão stream, central Portugal. Photographs taken in July 2019 (©Manuel A.S. Graça).

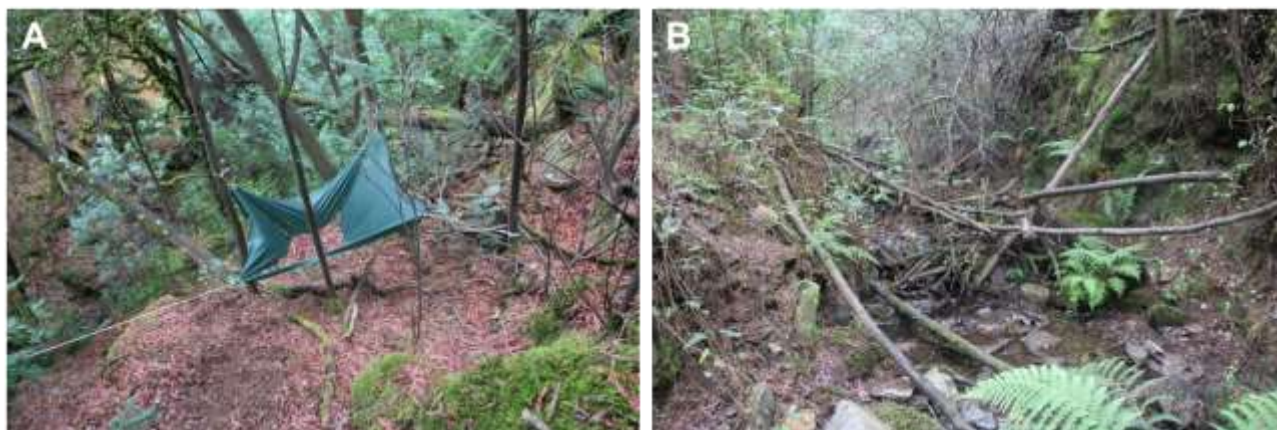


Fig. 6. Conceptual framework to predict effects of invasion of temperate deciduous broadleaf forests by N-fixing species on streams by considering a continuum from early to advanced stages of invasion by N-fixing species (e.g. *Acacia* spp.) of deciduous forests with (i) low and (ii) high representation 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).

