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LUÍS MÁRIO RIBEIRO

After an off-season fire: the behavior of exotic *Eucalyptus globulus* and invasive *Acacia longifolia* in Portugal

Andreia Anjos[1,2]; Joana Jesus[1,2]; Cristina Marques[3]; Nuno Borralho[3]; Helena Trindade[2]; Sérgio Chozas[2]; Cristina Máguas[2,*]

[1] Universidade de Lisboa, Faculdade de Ciências, Departamento de Biologia Vegetal, 1749-016 Lisboa, Portugal
[2] cE3c – Centre for Ecology, Evolution and Environmental Changes, Faculdade de Ciências, Universidade de Lisboa, 1749-016 Lisboa, Portugal; {cmhanson@fc.ul.pt}
[3] RAIZ – Forest and Paper Research Institute, 3800-783 Eixo, Portugal

**Corresponding author*

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Abstract

The introduction of species into exotic areas results in serious transformations on introduced areas. In Portugal, Eucalyptus globulus (exotic species) and Acacia longifolia (exotic invasive species) occupy a vast forested area. Eucalyptus globulus was extensively planted due to its role in pulpwood industries and, while the majority of plantations are managed, some are poorly managed along with isolated trees dispersed in the landscape (seed-trees) that are very huge and old, potentially increasing the risk of dispersal. Acacia longifolia was introduced for dune stabilization, but quickly expanded, becoming invasive without human intervention. As a leguminous species, the ability to establish symbiosis with nitrogen-fixing bacteria seems to be crucial to potentiate this invasiveness; however, these mutualistic interactions will interfere with soil microbiota, altering plant communities and affecting local biodiversity. Being two species adapted to post-fire regeneration, their behavior changes after fire occurrence, however after off-season fires, there is a gap in knowledge about their establishment dynamics. Eucalyptus globulus plantations and surrounding areas of seed-trees affected by June and October 2017 fire events were sampled, as well as unburnt areas. Acacia longifolia root-nodules were collected from unburnt and burnt areas affected by 2017 October fire and bacterial community was isolated and identified. Our results showed that the fire date and pre-fire management restrained E. globulus natural regeneration, with greater establishment in unmanaged plantations affected by the October fire. The presence of seed-trees seems to be less influenced by these factors (fire date and management), and can be considered an important seed source. Also, A. longifolia bacteriome has lower diversity after fire, but the main symbionts seem to be nitrogen-fixing bacteria, indicating a more specialized symbiosis that could enhance post-fire invasion. Bradyrhizobium spp. were the main partners in both studied zones, revealing its role as a facilitating microorganism. Off-season fires specific conditions seem to create more favourable conditions for E. globulus establishment, while A. longifolia seems to be able to establish promiscuous symbioses, but simultaneously adapt to a disturbed environment, managing to outcompete effectively with other plant species.

1. Introduction

Globally, the introduction of plant exotic species has increased due to economic interests and with ecosystems' rehabilitation purposes. However, these introduced species have negative impacts on novel ecosystems, such as disrupting ecosystems' functioning by altering water and soil cycles (Thompson *et al*., 2014; Liao *et al*., 2012), increasing fire hazard (Calviño-Cancela *et al*., 2018), reducing local biodiversity and modifying natural landscape (Vilà *et al*., 2011). In Portugal, the main exotic species are *Eucalyptus globulus* Labill. (Myrtaceae) and *Acacia longifolia* Andrews. (Leguminosae), two species native from Australia and introduced in the 19th century for different reasons (Alves *et al*., 2007; Peperkorn *et al.*, 2005). In the case of *E. globulus*, due to its fast growth, high productivity, and wood product quality (Turnbull, 1999), it was extensively planted for pulpwood production industries and occupies nowadays ca. one quarter of the forested area (ICNF, 2019). Most plantations have been planted intentionally and are managed with short rotation systems with 10-12 years tree cutting cycles and periodic clearing of the understory vegetation (Soares et al., 2007). Nonetheless, isolated *E. globulus* trees are often left uncut, hereafter referred as seed-trees, and many plantations are poorly managed, resulting in the presence of older trees with great reproductive capacity, potentially increasing the risk of

dispersal. However, *E. globulus* potential invasive capacity is a controversial topic, since qualitative studies classified it as invader in some parts of the world (Sanz-Elorza *et al*., 2001; Rejmánek and Richardson, 2013; Marchante *et al*., 2014), while other authors classified this species with a moderate risk of invasion, including in well managed plantations, which reduces its expansion beyond plantation edges (Larcombe *et al*., 2013; Fernandes *et al*., 2016; Ziller *et al*., 2018).

Another important exotic species is *A. longifolia*, considered nowadays as one of the most aggressive invaders, accounting with 18 % of the Portuguese mainland area occupied by alien species (Morais *et al*., 2017). This species was introduced for dune stabilization and recently, it has been described as an "ecosystem-engineer" (Stock *et al.*, 1995; Marchante *et al*., 2004; Yelenik *et al*., 2006) mostly determined by its inherent ability to fix atmospheric nitrogen through Legume–Rhizobia symbioses. Biological nitrogen fixation occurs inside root nodules, which includes a complex and reciprocal signalization process between the host plant and compatible bacteria (Andrews and Andrews, 2017). *Acacia* spp. do not have a specific bacterial partner, being a promiscuous woody species, that possibly exploits soil bacterial diversity to find partners for symbiotic success, particularly relevant in the context of invasion (Rodríguez-Echeverría *et al*., 2007; 2011). The identification of who is taking part in nodule's bacteriome remains a major challenge. Until now, several studies showed *Bradyrhizobium* as the most common partner in native and introduced environments, followed by *Rhizobium* (Rodríguez-Echeverría *et al*., 2010), while *Mesorhizobium* and *Sinorhizobium* appear mostly in the native range (Lafay *et al*., 2001; Marsudi *et al*., 1999; Nick *et al.*, 1999a, b). In fact, nitrogen-fixers are among the functional and taxonomically diverse rhizosphere communities (Kamutando *et al*., 2018).

Once *E. globulus* and *A. longifolia* are native from Australia, they are highly adapted to post-fire regeneration, both by bud resprouting and massive seed germination (Silva and Marchante, 2012; Águas *et al*., 2014, Calviño-Cancela *et al.*, 2018; Carvalho *et al*., 2010). In fact, fires are common perturbations in regions with Mediterranean type-climates (such as Portugal and Australia), characterized by long dry summers (Salis *et al.*, 2014). Under the current climate change scenario, it is known that the Mediterranean region will be undoubtably challenged, since it is expected an all year round warming more determinant in summer, and a widespread dryness ascribed to modifications in precipitation patterns (IPCC, 2021), resulting in a shift in fire regime extending the normal summer fire season (from July to September) with increasing off-season fires (Turco *et al*., 2019). For example, in Portugal, 2017 was a particularly dry and warm year, which resulted in several large wildfire events from June (early in the season) to mid-October (late in the season). As a consequence of the June fires ca. 52.000 hectares (ha) burned, while the October fires devastated an even larger area (ca. 190.000 ha) (ICNF, 2017). Fire events are a critical factor in these species' behavior, on one hand, regarding *E. globulus* dispersal dynamics that under off-season fires is still unknown and on the other hand, what happens on *A. longifolia* nodulation and bacterial diversity inside root nodules.

In this study, we aim to assess (1) the effects of off-season fires and pre-fire management alongside with the presence of seed-trees in *E. globulus* sapling dispersal and (2) if fire alters bacterial community inside *A. longifolia* root nodules.

2. Material and Methods

Eucalyptus globulus managed and unmanaged plantations and seed-trees surrounding areas were selected on areas affected by the off-season fires that occurred in June (early in the season) and in October (late in the season) of 2017 and in unburnt areas nearby; plots were sampled through distance transects composed by 3x3 m plots where sapling cover was assessed. Regarding *A. longifolia*, 5x5 m plots were selected in unburnt and burnt areas affected by October fire, where root nodules were collected by digging up saplings. Nodules were disinfected and bacterial diversity was isolated in YMA plates to identify symbiotic partners, through fingerprinting with M13 and rRNA 16S amplification.

Data analysis

Generalized Linear Mixed Model (GLMM) was performed in order to assess the factors that influenced *E. globulus* natural regeneration using Fire occurrence (No fire, June or October fire event), Management (managed and unmanaged) and Type (plantation or isolated seed-trees). To compare *A. longifolia* diversity between unburnt and burnt zones, Shannon-Wiener diversity index and Pielou evenness index were used.

3. Results and Discussion

3.1. *Eucalyptus globulus* behavior after off-season fire

Firstly, GLMM showed that Fire occurrence and pre-fire Management were the main factors influencing *E. globulus* saplings cover ($p < 0.001$). This species natural regeneration is very limited in absence of fire, since vegetation presence will compete with seedlings (Garau *et al.*, 2009) and litter accumulation constrain seedling emergence (Águas *et al*., 2017) (tab.1). After fire, seeds will find favorable conditions to germinate, however it is dependent on post-fire climatic conditions. In fact, after the June fire followed by summer months, regeneration was lower comparing with October fire followed by rainy season, given that seeds require wet and bare soil to germinate (Rejmánek and Richardson, 2011). However, pre-fire management highly restrain this species dispersal, since seed accumulation in the canopies is limited by frequent tree cutting cycles, preventing trees from reaching their full potential of seed production that occurs from 7 years old (Kirkpatrick, 1975). Furthermore, unmanaged conditions showed higher sapling cover especially after an October fire, representing the worst-case scenario, since trees are older leading to a greater accumulation of capsules up in the canopy. Additionally, seed-trees are an important propagules' source due to their age and seed production potential, being less sensitive to post-fire conditions and pre-fire management actions, influencing this species dispersal dynamics.

Table 1 – Eucalyptus globulus sapling cover (mean ± SE, %) for managed and unmanaged plantations and managed and unmanaged surrounding areas of seed-trees in absence of fire (no fire) and after June and October 2017 fires. Different letters indicate significant differences between no fire and the two fire dates (post hoc pairwise Tukey tests).

	Plantation		**Seed-tree**	
	Managed	**Unmanaged**	**Managed**	**Unmanaged**
No fire	0.58 ± 0.13^{a}	0.02 ± 0.02^{a}	0.07 ± 0.03^{a}	0.07 ± 0.04^{a}
June fire	0.10 ± 0.10^{ab}	1.38 ± 0.82^{ab}	2.56 ± 0.74^{ab}	9.35 ± 2.45^{cd}
October fire	1.70 ± 0.53^{a}	19.70 ± 4.35^{d}	6.72 ± 1.84^{bc}	14.00 ± 2.78^{e}

3.2. *Acacia longifolia* behavior after off-season fire

Considering *A. longifolia* nodulation, it seems that this process is potentiated after fire with a higher number of nodules present in young acacia saplings in post-fire environment (mean value of 14.0 comparing to 10.1 in unburnt zones), despite no statistically significant differences. However, there were differences in diversity and composition of bacteriome inside root nodules, with higher diversity present in unburnt zone (H' = 1.0) comparing to burnt zone (H' = 0.74) (tab. 2), underlining its promiscuity (Thrall *et al*., 2005). This higher diversity was expected once, under unburnt conditions, soils are inhabited by a greater abundance and diversity of bacteria in rhizospheric environment (Kamutando *et al*., 2018). After fire, symbiosis seems to be more specialized towards nitrogen-fixing bacteria, considering the disruption of plant-soil-biota feedbacks (Kulmatiski and Kardol, 2008) and a higher dominance of nitrogen-fixing bacteria observed. This more specialized bacteriome could be determinant for *A. longifolia* post-fire regeneration, increasing fitness, along with the absence of interspecific competition.

In this study, cultivable bacteria belonged to 5 different classes, including Alphaproteobacteria with *Bradyrhizobium* sp. as the most represented genera in both zones, Betaproteobacteria with *Paraburkholderia* sp. as the second most represented genera, and Gammaproteobacteria, mostly represented by *Pseudomonas* sp., from phylum proteobacteria; Actinobacteria from phylum actinobacteria and Bacilli from phylum firmicutes. Furthermore, there was also present an intraspecific diversity with *Bradyrhizobium cytisi* as the most abundant species in both zones.

Pielou evenness index showed a dominance of a genera in both unburnt and burnt zones (J' = 0.75 and J' = 0.67, respectively), which corresponds to the presence of *Bradyrhizobium* genus; in fact, this genus is the most common partner included among nitrogen-fixers and rhizobia group (Madigan and Martinko, 2006). Indeed, this genus has been already described as an important partner in native and introduced environments (Rodríguez-Echeverría *et al*., 2010), and its presence in both studied conditions reveals a close relationship with *A. longifolia* that may have a facilitating role. Furthermore, Paraburkholderia spp. and Pseudomonas spp. were also highly represented among isolates and are already included in Plant Growth Promoting Bacteria (PGPB), that could perform different functions apart from possible nitrogen fixation, once *Paraburkholderia* was already described

as nitrogen-fixing inducer and *Pseudomonas* was identified as non-rhizobial nodule inducing bacterial endophytes (NRE) (Martínez-Hidalgo and Hirsch, 2017). This apparently multifunctional bacteriome could be the reason why *A. longifolia* is such an effective invader.

Table 2 – Diversity of cultivated bacteria (%) isolated from A. longifolia root nodules from young saplings sampled in unburnt and burnt zones.

	Genera	Unburnt zone	Burnt zone
Alphaproteobacteria	*Althererythrobacter* sp.	1.0	0
	Bradyrhizobium sp.	36.2	45.8
	Paracoccus sp.	1.0	0
	Rhizobium sp.	1.0	0
Betaproteobacteria	*Caballeronia* sp.	2.0	0
	Duganella sp.	9.0	0
	Paraburkholderia sp.	16.0	13.6
Gammaproteobacteria	*Moraxella* sp.	2.0	0
	Pseudomonas sp.	13.8	10.2
Actinobacteria	*Micrococcus* sp.	2.0	6.8
	Nocardioides sp.	1.0	1.6
Bacilli	*Paenibacillus* sp.	2.0	0
-	Not identified	13.0	22.0

4. Conclusions

Fire seems to have a determinant role in these exotic species behavior in studied areas, influencing dispersal dynamics of *E. globulus* and altering *A. longifolia* bacteriome inside nodules. *Eucalyptus globulus* establishment is highly dependent on fire occurrence and also on post-fire climatic conditions, but also the management practices implemented prior to fire. It is important to highlight the potentiated dispersal after October fire, as well as, the presence of seed-trees as a key propagule source. Furthermore, *A. longifolia* symbiosis seems to be influenced by fire, with a more specialized interaction with nitrogen-fixing bacteria that can be referred as the "first settlers" within symbiosis reestablishment after fire. However, unburnt conditions highlighted for the fact that this invasive species is a generalist mutualist, capable of establishing symbiosis with a greater diversity of rhizospheric bacteria.

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