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Suppression of an invasive pine by a native shrub following a megafire

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Abstract

Seedling density of the Chilean wineberry *Aristotelia chilensis* negatively correlates with the seedlings' abundance of an invasive pine *Pinus radiata*, particularly in post-fire areas. This pattern emerged following a megafire in Chile's Coastal Maulino Forest, a biodiversity hotspot facing increasing fire threats. This pattern, coupled with a high proportion of plots lacking pine seedlings, suggests that *A. chilensis* may play a role in limiting *P. radiata* invasion. The negative relationship was strongest in areas with moderate fire severity, likely reflecting differences in shade tolerance. *A. chilensis*, a light-demanding species with some degree of shade tolerance, can persist in partially shaded environments. In contrast, *P. radiata*, a more strictly light-demanding species, struggles to establish under significant shade. In high-severity fires, however, we found no significant relationship between these species, likely due to detrimental effects on both species, including potential microbiome dependence for *A. chilensis*. As *A. chilensis* shows successful establishment at low fire severity, enhancing its post-fire recruitment, particularly in moderately burned areas, could be a valuable strategy for mitigating *P. radiata* invasion and restoring fire-affected Mediterranean ecosystems.

Keywords

Invasion resistance, Fire severity, Post-fire establishment, Soil microbiome

Introduction

Wildfires pose a significant threat to biodiversity, disrupting ecosystem functions and threatening sensitive habitats worldwide. Their increased frequency and intensity are attributed to various factors, including climate change and land-use modifications (McLauchlan et al. 2020). The Coastal Maulino Forest, a biodiversity hotspot in central Chile (Myers et al. 2000), is facing more frequent and intense wildfires in last decades, driven by factors such as rising temperatures, a megadrought and the forestry plantations of non-native species (González et al. 2018, 2023), some of which could become invasive after fire disturbances. Primarily, the invasive species is *Pinus radiata* (Pinaceae) which covers approximately 60% of the country's 2.5 million hectares of forest plantations (Bustamante and Simonetti 2005, González et al. 2018). The devastating 2017 "Las Máquinas" megafire burned over 200,000 ha of the Coastal Maulino Forest, a stark reminder of the vulnerability of this ecosystem (Valencia et al. 2018). Despite ongoing active and passive restoration efforts in south-central Chile (Morales et al. 2021, Souza-Alonso et al. 2022), challenges persist, including the rapid arrival of post-fire pine regeneration that hinders restoration success (Gómez et al. 2019, González et al. 2020, 2023). This highlights the need for conservation and restoration practices tailored to this unique ecosystem.

Invasive species often display rapid resource utilisation, potentially outcompeting native species and promoting more frequent fire events. This can create a positive invasion-fire feedback loop (Contreras et al. 2011, Taylor et al. 2017). *P. radiata* is a light-demanding and shade-intolerant species known for its aggressive post-fire regeneration through serotinous cones, which release large amounts of viable wind-dispersed seeds after fire events (Franzese and Raffaele 2017). Studies have shown a higher probability of fire ignition in areas dominated by *P. radiata* plantations compared to native forests in south-central Chile (Contreras et al. 2011, Gómez-González et al. 2019).

Previous research suggests limited success in controlling *P. radiata* invasion through overall native species diversity (Gómez et al. 2019, González et al. 2020). However, recent field studies provide evidence that the native wineberry species *Aristotelia chilensis* (Elaeocarpaceae) efficiently recolonises burnt areas even where *P. radiata* is present (Promis et al. 2019, Becerra et al. 2022). *A. chilensis* is a fast-growing, light-demanding, fleshy-fruiting bird-dispersed tree species with a semi-dioecious leaf habit. These traits allow it to not only colonise clearings but also persist after plantations replace native forests because it can exhibit some shade tolerance (Guerra et al. 2010, Salgado-Luarte and Gianoli 2012). This rapid establishment and fast growth of *A. chilensis* would align with the concept of the "pre-emptive resource effect" – a mechanism where early colonising native species can outcompete invasive plants by monopolising essential resources (Byun et al. 2013, Byun and Lee 2017, Delavaux et al. 2023). Additionally, studies suggest that *P. radiata*, being a shade-intolerant species, might struggle to establish into a darker understory dominated by *A. chilensis* and other native species (Gómez et al. 2019, Becerra and Simonetti 2020). The efficient colonisation and fast growth of *A. chilensis* suggest that it has the potential to act as a native plant competitor against *P. radiata* invasion in fire-affected ecosystems.

Building upon competition-based biotic resistance (Elton 1958) and the theory of limiting similarity, where native species can limit invasive plant establishment due to niche overlap, we hypothesised that *P. radiata* abundance would negatively correlate with increasing *A. chilensis* abundance. Specifically, we tested the relationship between the abundance of *A. chilensis* and *P. radiata* in plots affected by varying fire severity levels caused by the Las Máquinas mega-fire in the Maulino Coastal Forest. Additionally, we explored whether fire severity modulates this relationship. Moderate- or low-severity fires that increase light penetration while retaining understory vegetation could favour *A. chilensis* establishment, potentially strengthening its competitive effect on *P. radiata* (i.e., a negative relationship). In contrast, high-severity fires that create harsher conditions and potential soil disruption (i.e., depleting the soil microbiome) could hinder the establishment of both *A. chilensis* and *P. radiata*, obscuring any competitive effects. By elucidating these dynamics, we aim to provide valuable data to guide and enhance conservation and restoration efforts in fire-affected areas across the central Mediterranean region of Chile.

Materials and methods

Study Site

The study was conducted at El Porvenir (35°42' S, 72°22' W), located at the northern edge of the Coastal Maulino Forest in central-south Chile (Gómez et al. 2022). El Porvenir is a fragment of native mesic forest type, surrounded by large stands of planted *P. radiata* and *Eucalyptus globulus* (Myrtaceae). The dominant tree species include *Nothofagus glauca* (Nothofagaceae), *N. alessandrii*, *N. obliqua*, *Cryptocarya alba* (Lauraceae), *Aextoxicon punctatum* (Aextoxicaceae), *Gevuina avellana* (Proteaceae), and *A. chilensis*. Study area has a Mediterranean climate with a mean annual precipitation of 918 mm and a mean annual temperature of 12.7 °C (Becerra and Simonetti 2020).

In January 2017, the Las Máquinas megafire affected El Porvenir, which experienced fire severity ranging from low to high (see Valencia et al. 2018, Gómez et al. 2022). Following the fire, several species exhibited regeneration at different levels, with high seedling recruitment for the invasive *P. radiata* and the native *A. chilensis* (Gómez et al. 2022).

Plot establishment and seedling survey

To assess the potential role of *A. chilensis* in limiting *P. radiata* invasion, we established twenty-three 625 m^2 plots across El Porvenir. These plots were randomly distributed within areas experiencing low (n = 8), moderate (n = 10), and high (n = 5) fire severity (see Gómez et al. 2022). Seedling surveys were conducted at 8 and 24 months following the Las Máquinas mega-fire (hereafter 2017 and 2019). To estimate the density of *A. chilensis* and *P. radiata* seedlings, three 1 m^2 sub-plots were randomly located within each plot to search for regenerating *A.chilensis* and *P. radiata* seedlings under 60 cm in height. The average number of seedlings per 3 m^2 sampled area was 21.98 ± 20.34 for *A. chilensis* and 7.46 ± 12.78 for *P. radiata*. To confirm that the seedlings originated from seeds and not resprouts, we collected at least three random plant samples per species from each sub-plot for root system examination.

Data analysis

We performed a negative binomial Generalised Linear Mixed-effects Model (NB GLMM) to analyse the relationship between the abundance of *A. chilensis* and *P. radiata* seedlings. This statistical method is suitable for counting data with overdispersion, a common characteristic of ecological data. Here, we account for the potential influence of sampling time at each plot by including time since the fire as a random factor nested within fire severity. This nested structure considers the variation in fire severity across the landscape while acknowledging the potential influence of sampling time within each fire severity category (see above). Additionally, we conducted separate NB GLMM analyses for each fire severity level, including time sampling as a random factor.

Results and Discussion

Our analysis revealed a negative relationship between *A. chilensis* and *P. radiata* abundance across the study site ($\chi^2_{(1,46)} = 8.0707$, $p < 0.01$; Fig. 1). Thus, areas with higher numbers of *A. chilensis* seedlings have fewer *P. radiata* seedlings, potentially indicating a suppressive effect of native species on invasive tree establishment.

Furthermore, our results suggest that the strength of this negative relationship varied depending on fire severity. A significantly negative relationship between *A. chilensis* and *P. radiata* was found in areas with moderate fire severity ($\chi^2_{(1,20)} = 16.385$, $p < 0.01$; Fig. 2). In contrast, these two species had no significant relationship in plots with high or low fire severity (Fig. 2). This pattern hints that fire severity might play a role in mediating the interaction between *A. chilensis* and *P. radiata*. Wildfire severity plays a crucial role in shaping post-fire succession and ecosystem dynamics. Understanding the severity-specific effects of fires is essential for developing effective forest restoration and conservation management strategies.

The observed negative correlation between the abundance of *A. chilensis* and *P. radiata* suggests that the former's presence, as a component of the pre-fire native flora, can be considered a predictor variable influencing *P. radiata* establishment in post-fire areas. Given that *A. chilensis* was already present in these ecosystems before the fires, its abundance at the time of the fire event likely influenced the available resources and habitat conditions for *P. radiata* establishment. Several mechanisms could explain this phenomenon, including the priority effect by pre-empting resources and habitat filtering (Byun et al. 2013, Byun and Lee 2017). First, *A. chilensis* is a fast-growing, light-demanding species. In areas with a higher abundance of *A. chilensis*, competition for light, water, or nutrients could be hindering the successful establishment of *P. radiata* seedlings. Future studies that quantify resource availability and seedling performance concerning *A. chilensis* density could provide stronger evidence for this hypothesis. Second, fire can have profound and different effects on plant community assembly depending on its severity (McLauchlan et al. 2020). The environmental conditions created by moderate fire severity may be more favourable for the establishment of native compared to invasive species. Specifically, these fires create a more open canopy with increased light availability in the understory, typically forming a patchy mosaic of burned and unburned areas rather than eliminating the entire canopy. While *A. chilensis* is a light-demanding species with some degree of shade tolerance (Guerra et al. 2010, Salgado-Luarte and Gianoli 2012), *P. radiata* is a strictly shade-intolerant species (Gómez et al. 2019). Thus, this variation in light availability could favour *A. chilensis* over *P. radiata* establishment in suitable microsites within the burned landscape. In low-severity fires with more remaining canopy cover, *P. radiata* pine showed very low establishment (only two plots with 9 and 15 seedlings), likely due to limited light availability for germination and seedling growth. In contrast, *A. chilensis*, which can exhibit some shade tolerance, could persist and thrive, with an average of 16 seedlings per plot and up to 67 in one case (Fig. 2). High-severity fires present a vastly different scenario, where most or all vegetation is fire-consumed and heat sterilises the soil, eliminating vital microbes and disrupting biogeochemical processes. These harsh conditions are detrimental to the establishment of both species, resulting in the lack of relationship observed in Fig. 2. In this line, *A. chilensis*'s lower establishment suggests a dependence on healthy soil microbes (Escobedo et al. unpublished), which are eliminated by high-severity fires. *P. radiata*, meanwhile, sometimes showed higher abundance in these areas, potentially benefiting from the open and *A. chilensis*-free conditions since its establishment and survival are less reliant upon microbe communities (Escobedo et al. unpublished). This resilience disparity highlights the threat of high-severity fires to the Coastal Maulino forest.

Our findings suggest that native *A. chilensis* might play a role in limiting *P. radiata* invasion, potentially through competition and/or habitat filtering. However, this beneficial effect might be compromised in high-severity fire areas, where *A. chilensis* establishment is hampered due to its dependence on a healthy soil microbiome. High-severity fires that disrupt soil microbial communities pose a significant threat to native plant communities and their ability to resist invasion. Promoting the establishment of native species like *A. chilensis*, particularly in areas with moderate fire severity, could be a valuable strategy for mitigating tree invasion and fostering the recovery of fire-affected Mediterranean ecosystems like the Maulino forest in central Chile.

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Data Availability

The data supporting this study's findings will be available in a repository upon manuscript acceptance.

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Figures

Figure 1. Model-predicted relationship between *Aristotelia chilensis* and *Pinus radiata* seedlings abundance for two sampling times (2017 and 2019). Line indicates a statistically significant negative relationship ($p < 0.05$) based on a negative binomial GLMM.

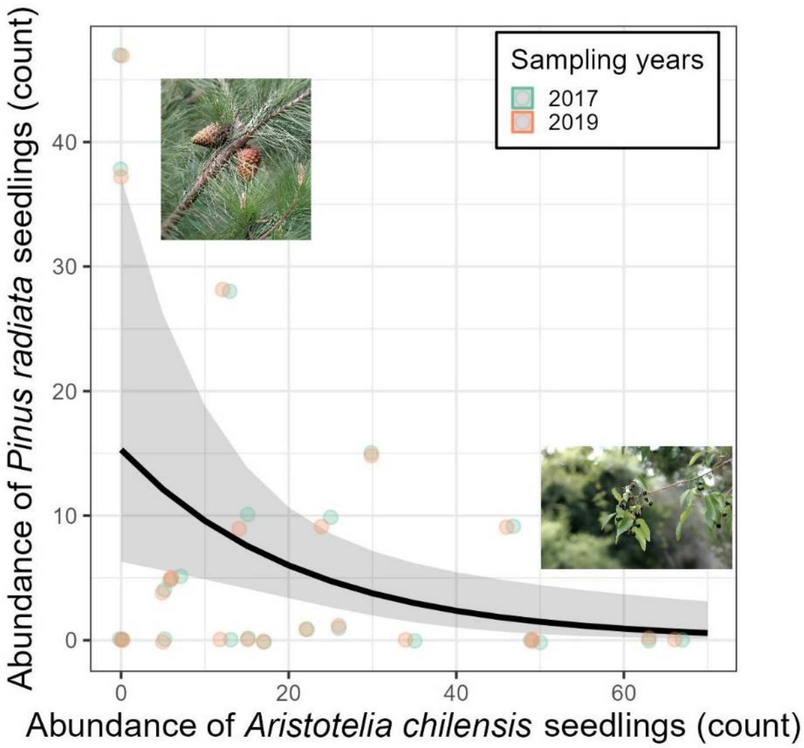

Figure 2. Model-predicted relationships between *Aristotelia chilensis* and *Pinus radiata* seedling abundance across fire severity levels (a, low; b, medium; c, high) for two sampling times (2017 and 2019). The solid line in the middle panel (b, moderate-severity fire area) indicates a statistically significant negative relationship ($p < 0.05$) based on a negative binomial GLMM. Relationships were not statistically significant in high- or low-fired-severity areas.