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Post-fire negative relationship between a native tree and an invasive pine at the Coastal Maulino Forest in Central Chile

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Coastal Maulino Forest, a biodiversity hotspot, is increasingly threatened by frequent and higher-severity wildfires. Endangered tree species, including *Nothofagus* spp., inhabit small, isolated native forest fragments surrounded by extensive *Pinus radiata* plantations, a non-native species that often colonises fire-affected areas. However, the seedling density of the native Chilean wineberry, *Aristotelia chilensis*, negatively correlates with the abundance of *P. radiata* seedlings in post-fire areas. This pattern emerged across areas burned at varying fire severities, sampled 8 and 24 months following the 2017 “Las Máquinas” megafire in Chile. The high proportion of plots lacking *P. radiata* seedlings, coupled with this negative relationship, suggests that *A. chilensis* may play a role in limiting *P. radiata* invasion. The negative relationship was most pronounced in areas with moderate fire severity, likely reflecting differences in shade tolerance between the species. While *A. chilensis*, a light-demanding species with some shade tolerance, can persist in partially shaded environments, *P. radiata*, a strictly light-demanding species, struggles under significant shade. In low-severity areas, no significant relationship was observed since the substantial native canopy remaining likely limits *P. radiata* establishment by shading. Conversely, in high-severity fire areas, the absence of a significant relationship might result from the detrimental effects on both species, including potential microbiome dependence for *A. chilensis*. Given the successful establishment of *A. chilensis* 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, Coastal Maulino Forest, 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 severity 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), has experienced more frequent and higher-severity wildfires in recent decades, driven by rising temperatures, a megadrought, and extensive forestry plantations of non-native species (González et al., 2018, 2023), some of which become invasive after fire disturbances. These fires are particularly concerning for the survival of endangered species such as *Nothofagus alessandrii* (Nothofagaceae) and *N. glauca*, which are confined to small, isolated forest fragments surrounded by vast *Pinus radiata* (Pinaceae) plantations. The invasive *P. radiata*, which covers approximately 60% of the country's 2.5 million hectares of forest plantations (Bustamante and Simonetti, 2005; González et al., 2018), often rapidly colonises post-fire areas, further endangering these native species. The devastating 2017 “Las Máquinas” megafire burned over 200,000 ha of the Coastal Maulino Forest, underscoring 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; Gómez and Garrido, 2018). 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) can efficiently recolonise burnt areas, often where *P. radiata* seedlings are sparse or absent (Promis et al., 2019; Becerra et al., 2022). *A. chilensis* is a semi-dioecious, fast-growing, light-demanding, fleshy-fruited, bird-dispersed, evergreen small tree species. 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 Coastal Maulino 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*. The 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).

The total plant species richness at El Porvenir is 104 species, with Asteraceae and Fabaceae being the most representative families. Growth forms within the forest include herbs, shrubs, trees, and climbers. In the understory, in addition to *A. chilensis*, notable species include *Solanum crispum*, *Carex phleoides*, *Francoa appendiculata*, *Polystichum chliensis*, *Escallonia illinita*, *Dioscorea brachybotria*, *Colletia ulicina*, *Pteris chilensis*, *Ageratina glechnophylla*, *Baccharis racemosa*, *Retanilla ephedra*, *Tropaeolum ciliatum*, *Boquila trifoliolata*, *Pseudognaphalium vira-vira*, *Epilobium ciliatum*, *Sanicula crassicaulis*, *Synammia feullei*, *Lathyrus cabrenianus*, *Baccharis concava*, *Dioscorea humifusa*, *Sophora macrocarpa*, *Senna stipulacea* and *Rhaphythamnus spinosus*, among others.

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).

Fire severity assessment

Fire severity at the study site was estimated from plots established in March 2017 using the Composite Burn Index (CBI), following the protocol of Key and Benson (2006) (see Gómez et al., 2022). In twenty-three 625 m² plots randomly established across El Porvenir, we evaluated five vertical strata (soil, herbs, shrubs, intermediate trees, and large trees) arranged in a hierarchical structure (De Santis and Chuvieco, 2007). At each stratum, visual attributes were assessed, including changes in colour due to fire, litter and surface fuels, canopy cover alterations, and vegetation mortality (De Santis and Chuvieco, 2009). These attributes were used to generate CBI values for each plot, which were then classified into three severity categories: low (minimal changes in cover and low vegetation mortality, n = 8), moderate (a mix of unchanged and highly altered cover, n = 10), and high (extensive to complete vegetation mortality, n = 5). The mean values of the attributes for each plot were used to compile a composite CBI score.

Plot establishment and seedling survey

To assess the potential role of *A. chilensis* in limiting *P. radiata* invasion, we used the previously established twenty-three plots across El Porvenir. As noted in the “Fire severity assessment” section, these plots were randomly established across the forest fragment, covering a range of distances from surrounding pine plantations. Although the distance from pine seed sources was not explicitly analysed, the random establishment ensured a representation of various distances, thereby minimising potential bias in plot location. In each plot, seedling surveys were conducted at 8 and 24 months following the Las Máquinas mega-fire (hereafter 2017 and 2019), meaning the same plots were revisited to assess changes over time. To estimate the density of *A. chilensis* and *P. radiata* seedlings, three 1 m² sub-plots were randomly located within each plot to survey all *A. chilensis* and *P. radiata* seedlings that had regenerated (not resprouted) and were under 60 cm in height. The average number of seedlings per 3 m² 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. While *P. radiata* is not known to resprout after fire, *A. chilensis* may exhibit resprouting behaviour (Gómez, 2019), which was accounted for during root 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 (2017 and 2019) 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 *Aristotelia chilensis* and *Pinus radiata* abundance across the study site ($\chi^2_{(1,46)} = 8.0707$, $p < 0.01$; Figure 1). Areas with higher numbers of *A. chilensis* seedlings had fewer *P. radiata* seedlings, suggesting a potential suppressive effect of native small tree species on the establishment of the invasive tree.

This negative relationship between *A. chilensis* and *P. radiata* was especially pronounced in areas with moderate fire severity ($\chi^2_{(1,20)} = 16.385$, $p < 0.01$; Figure 2), whereas no significant relationship was observed in plots with high or low fire severity (Figure 2). These findings suggest that fire severity may mediate the interaction between *A. chilensis* and *P. radiata*, with moderate fire severity favouring the competitive advantage of native species. Fire severity is known to shape post-fire succession and ecosystem dynamics, making it crucial to understand these effects for both effective forest restoration and conservation management strategies.

In addition to *A. chilensis*, other native species, particularly the endangered *Nothofagus alessandrii* and *N. glauca*, are acknowledged components of the Coastal Maulino Forest. These species, such as *A. chilensis*, are part of the pre-fire native flora, and their presence may contribute to post-fire regeneration dynamics. However, both *N. alessandrii* and *N. glauca* face particular challenges in regenerating after fires, especially in areas with high-severity burns (Gómez et al., 2022). The severe disruption of soil conditions and the elimination of key microbial communities could limit their recovery (Certini, 2005; Warneke et al., 2023; Escobedo et al., 2024), further threatening the ecological integrity of these fragmented populations (Gómez et al., 2022; González et al., 2023). Given their importance, restoration efforts must consider the regeneration of fast-growing species like *A. chilensis*, which may support strategies for the recovery of slow-growing, fire-sensitive species such as *N. alessandrii* and *N. glauca*.

The observed negative relationship between *A. chilensis* and *P. radiata* suggests that the former's presence, as a component of the pre-fire native flora, may influence *P. radiata* establishment in post-

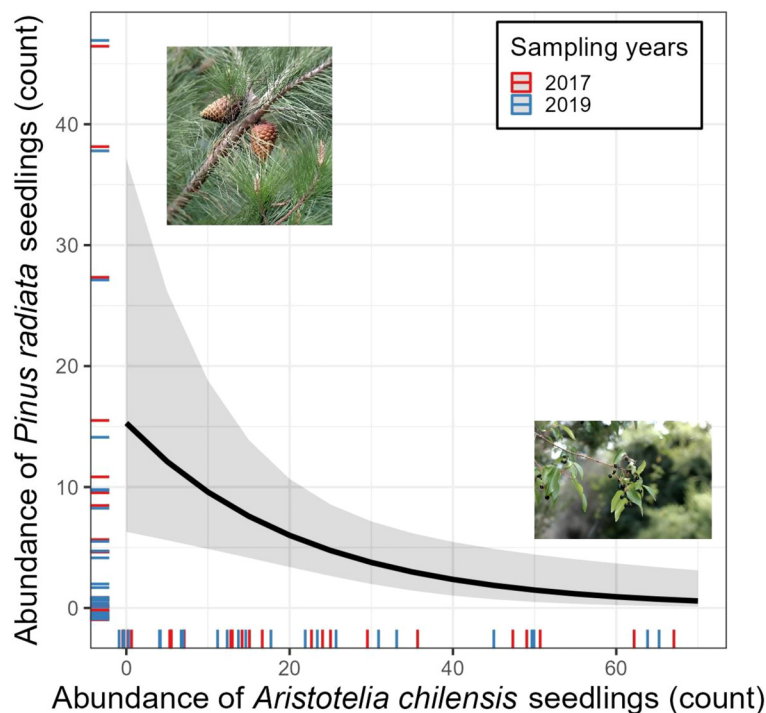


FIGURE 1

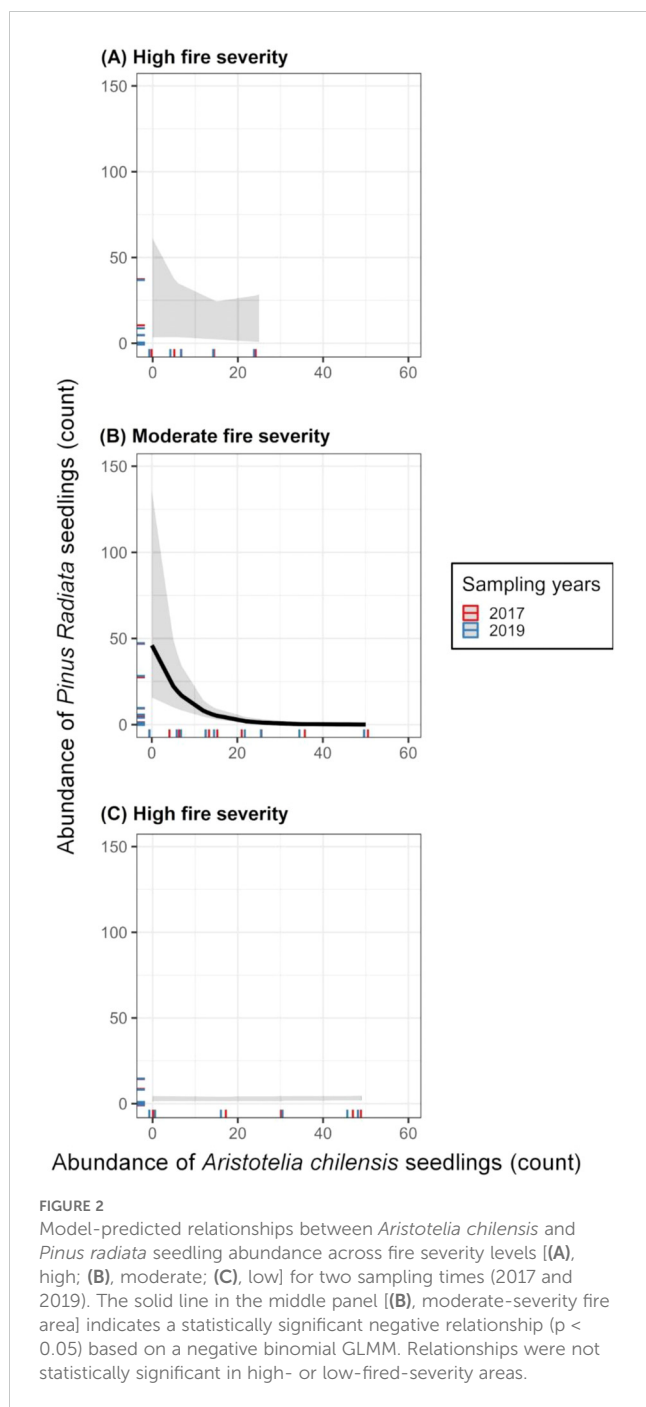
Model-predicted relationship between *Aristotelia chilensis* and *Pinus radiata* seedlings abundance for two sampling times (2017 and 2019). Line indicates a statistically significant negative relationship ($p < 0.05$) based on a negative binomial GLMM.

fire areas. As *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, including the priority effect by pre-empting resources and habitat filtering (Byun et al., 2013; Byun and Lee, 2017). Given that *A. chilensis* is a fast-growing, light-demanding species, it may pre-empt light, water, or nutrients in areas where it is abundant, hindering *P. radiata* establishment. Future studies quantifying resource availability and seedling performance in relation to *A. chilensis* density could provide stronger evidence for this hypothesis.

Moreover, 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 (Figure 2). Consequently, the lingering native canopy foliage after low-severity fires probably limits light availability, thus restricting the establishment of *P. radiata* seedlings.

High-severity fires present a vastly different scenario because nearly all vegetation is fire-consumed and heat sterilises the soil, eliminating vital microbes and severely disrupting biogeochemical processes. In these harsh conditions, the establishment of *A. chilensis* and *P. radiata* is hindered, resulting in the lack of relationship observed in Figure 2. In this line, *A. chilensis*'s lower establishment suggests a dependence on healthy soil microbes (Escobedo et al., 2024), which are eliminated by high-severity fires. *P. radiata*, meanwhile, sometimes showed higher abundance in these areas, potentially benefiting from the transiently increased nutrient availability and *A. chilensis*-free conditions since its establishment and survival are less reliant upon microbe communities (Escobedo et al., 2024). This resilience disparity in high-severity fire areas poses a significant threat to the already vulnerable Coastal Maulino Forest, especially for endangered species such as *N. alessandrii* and *N. glauca* that are less adapted to such extreme and changing conditions. Although the general trends observed in areas of high fire severity are consistent with our expectations, we acknowledge that the small number of high-severity plots ($n=5$) may limit the statistical power to detect finer-scale interactions between *A. chilensis* and *P. radiata* in these areas.



This limitation should be addressed in future studies with a larger number of high-severity plots to confirm the patterns observed. Furthermore, more extensive sampling could improve our understanding of how fire severity impacts post-fire recovery dynamics in native and invasive species.

To expand on the implications of long-term competition dynamics at the Coastal Maulino Forest, it is important to consider that the competitive interactions between *A. chilensis* and *P. radiata* may shift over time. While our study captured early successional processes in the first two years post-fire, we speculate that as *A. chilensis* continues to establish and grow, it may

increasingly outcompete *P. radiata* in the coming years due to its superior shade tolerance. Conversely, in areas where *P. radiata* manages to establish initially, its rapid growth may enable it to outcompete *A. chilensis* over time. Active management strategies that include the removal of *P. radiata* seedlings in the early stages, combined with the promotion of *A. chilensis*, could provide a highly effective restoration approach. Restoration techniques promoting *A. chilensis* recruitment—such as direct seedling planting with native soil microbiomes, boosting seed dispersal, and optimizing environmental factors like light and soil conditions—could be pivotal in encouraging its establishment post-fire. This dual strategy may not only suppress invasive *P. radiata* populations but also support the long-term recovery of native ecosystems, fostering the establishment of fire-sensitive species like *N. alessandrii* and *N. glauca*. Long-term monitoring of these interactions would be essential to confirm whether the trends observed in the short term persist or evolve in different fire severity scenarios.

While our study focused on the Las Máquinas 2017 megafire, the findings possess broader implications beyond the Coastal Maulino Forest, particularly in regions experiencing increased fire frequencies where *P. radiata* is invasive. Similar interactions between native and invasive species have emerged in other Mediterranean-type ecosystems, such as those in California (Dimitrakopoulos and Papaioannou, 2001; Alexander and D'Antonio, 2003) or Australia (Grice, 1997), and South Africa (Van Wilgen and Richardson, 1985; Holmes et al., 2000), where variable fire frequencies and species compositions influence competition dynamics. In areas such as Hawaii, Australia, and New Zealand (Mandle et al., 2011; Hynson et al., 2013), the spread of *P. radiata* and resultant fire-induced disturbances present parallel challenges. These comparisons underscore the necessity of factoring ecosystem-specific characteristics into our understanding of post-fire recovery. The competitive dynamics observed between native species such as *A. chilensis* and *P. radiata* could inform management strategies aimed at controlling pine invasions across diverse regions. Although our study concentrated on the Coastal Maulino Forest, the mechanisms of native species pre-empting resources and moderating invasive species establishment (e.g., competition for resources, shading effects) might be applicable to other ecosystems with similar invasion and fire dynamics (e.g., Grace, 1998; Brooks et al., 2004). Further research is essential to comprehensively understand how native species can be leveraged to manage *P. radiata* invasions effectively in varying fire-prone environments.

Conclusions

Our findings suggest that promoting the establishment of native species like *A. chilensis*, particularly in areas with moderate fire severity, could help limit the invasion of *P. radiata*. Thus, restoration strategies might consider *A. chilensis* as a targeted support species for the recovery of fire-sensitive species such as *N. alessandrii* and *N. glauca*, which are crucial for maintaining the ecological integrity of the Coastal

Maulino Forest. Moreover, this study highlights potential applications beyond this region, offering insights into managing *P. radiata* invasions in other fire-prone ecosystems worldwide. Efforts focused on enhancing post-fire recruitment of *A. chilensis*, especially in areas of moderate fire severity, could offer a pathway to mitigating invasive tree spread and promoting ecosystem recovery in this unique biodiversity hotspot.

Data availability statement

The original contributions presented in the study are publicly available. This data can be found here: <https://doi.org/10.6084/m9.figshare.27640251.v1>.

Author contributions

VE: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. PG: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Validation, Writing – review & editing. MM: Conceptualization, Resources, Supervision, Validation, Writing – review & editing. IA: Funding acquisition, Project administration, Resources, Supervision, Writing – review & editing.

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Conflict of interest

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