




REVIEW

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A review of fire effects across South American ecosystems: the role of climate and time since fire

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Abstract

Background: Fire is an important driver of ecosystem dynamics worldwide. However, knowledge on broad-scale patterns of ecosystem and organism responses to fires is still scarce. Through a systematic quantitative review of available studies across South America, we assessed fire effects on biodiversity and abundance of different organisms (*i.e.*, plants, fungi, invertebrates, and vertebrates), plant fitness, and soil properties under four climate types, and time since the last fire (*i.e.*, early and late post fire). We addressed: (1) What fire effects have been studied across South America? (2) What are the overall responses of biodiversity, abundance, fitness, and soil properties to fires? (3) How do climate and time since fire modulate those responses?

Results: We analyzed 160 articles reporting 1465 fire responses on paired burned and unburned conditions. We found no effect of fire on biodiversity or on invertebrate abundance, a negative effect on woody plant species and vertebrate abundance, and an increase in shrub fitness. Soil in burned areas had higher bulk density and pH, and lower organic matter and nitrogen. Fire effect was significantly more positive at early than at late post fire for plant fitness and for soil phosphorus and available nitrogen. Stronger negative effects in semiarid climate compared to humid warm climate suggest that higher temperatures and water availability allow a faster ecosystem recovery after fire.

Conclusions: Our review highlights the complexity of the climate–fire–vegetation feedback when assessing the response of soil properties and different organisms at various levels. The resilience observed in biodiversity may be expected considering the large number of fire-prone ecosystems in South America. The recovery of invertebrate abundance, the reduction of the vertebrate abundance, and the loss of nitrogen and organic matter coincide with the responses found in global reviews at early post-fire times. The strength of these responses was further influenced by climate type and post-fire time. Our synthesis provides the first broad-scale diagnosis of fire effects in South America, helping to visualize strengths, weaknesses, and gaps in fire research. It also brings much needed information for developing adequate land management in a continent where fire plays a prominent socio-ecological role.

Keywords: abundance, biodiversity, biomass, climate, effect size, fire impact, fire response, fitness, meta-analysis, soil properties

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Resumen

Antecedentes: El fuego es un importante modulador de la dinámica de los ecosistemas en el mundo. Sin embargo, el conocimiento a gran escala de los patrones de respuesta de ecosistemas y organismos es aún escaso. A través de una revisión sistemática cuantitativa de los estudios disponibles a lo largo de Sudamérica, abordamos los efectos del fuego sobre la biodiversidad, abundancia de diferentes organismos (*i.e.*, plantas, hongos, invertebrados y vertebrados), aptitud de las plantas y propiedades del suelo bajo diferentes condiciones climáticas (*i.e.*, cuatro tipos climáticos), y tiempo transcurrido desde el último incendio (*i.e.*, tiempo post-fuego temprano y tardío). Respondimos: (1) ¿Qué efectos del fuego se han estudiado en Sudamérica? (2) ¿Cuáles son las respuestas generales de la biodiversidad, abundancia, aptitud y propiedades del suelo al fuego? (3) ¿Cómo el clima y el tiempo post-fuego modulan esas respuestas?

Resultados: Analizamos 160 artículos que reportaron 1465 respuestas al fuego de sitios apareados quemados y no quemados. No encontramos efectos del fuego sobre la biodiversidad y abundancia de invertebrados, encontramos efectos negativos sobre la abundancia de especies de plantas leñosas y de vertebrados, y un incremento en la aptitud de los arbustos. El suelo en sitios quemados tuvo mayor densidad aparente y pH, y menor materia orgánica y Nitrógeno. El efecto del fuego fue significativamente más positivo en tiempos post-fuego tempranos que en tardíos para aptitud de las plantas, y para el Fósforo y Nitrógeno disponible del suelo. Además, encontramos efectos negativos más fuertes en climas semiáridos que en climas húmedos cálidos, sugiriendo que altas temperaturas y disponibilidad de agua permiten una mayor recuperación de los ecosistemas después del fuego.

Conclusiones: Nuestro estudio destaca la complejidad de las relaciones clima–fuego–vegetación para abordar las respuestas de las propiedades del suelo y de diferentes organismos a varios niveles. La resiliencia observada en la biodiversidad puede ser esperada dado el alto número de ecosistemas propensos al fuego en Sudamérica. La recuperación de la abundancia de invertebrados, la reducción de la abundancia de vertebrados, y las pérdidas de Nitrógeno y Materia Orgánica coincide con las respuestas encontradas en revisiones globales en tiempos cortos después del fuego. La tendencia de estas respuestas estuvo además influenciada por el tipo de clima y tiempo post fuego. Nuestra síntesis provee el primer diagnóstico a gran escala de los efectos del fuego en Sudamérica, ayudando a visualizar las fortalezas, debilidades y vacíos en los estudios del fuego. También brinda información muy necesaria para el desarrollo de estrategias adecuadas de manejo en un continente en el cual el fuego juega un papel socio-ecológico preponderante.

Introduction

Fire is an important driver in the dynamics of terrestrial ecosystems, influencing many attributes, functions, and processes (Bowman et al. 2009; Staver et al. 2011; Archibald et al. 2018). Fire triggers ecosystem succession, causing traceable changes in attributes such as biodiversity at different trophic levels (Pausas and Keeley 2009; He et al. 2019), abundance (Pausas and Ribeiro 2017; Carbone et al. 2019), fitness (García et al. 2016; Carbone and Aguilar 2017), as well as soil properties (Certini 2005; Pellegrini et al. 2018). Understanding these changes imposed by fire is challenging, as there are several factors involved that act at different spatial and temporal scales (Bowman et al. 2009; Archibald et al. 2013; Harris et al. 2016; Pausas and Dantas 2017).

Feedbacks between climate, vegetation, and fire often involve complex non-linear and context-dependent relationships, influencing ecological processes and evolutionary aspects of the biota, which in turn influence ecosystem responses to fire (Pausas and Paula 2012; Archibald et al. 2013, 2018; Miller et al. 2013; Pausas and Ribeiro 2013, 2017). Climate, which defines gradients of temperature

and moisture, is a strong regulator of ecosystem properties and plant traits, such as biomass, leaf area, and net primary productivity (Whittaker and Marks 1975; Bond et al. 2005; Pausas and Ribeiro 2013). Fire activity is linked to the productivity–aridity gradient imposed by climate, in which conditions at either end of the gradient are less conducive to fire, either due to excess of moisture (high-productivity extreme) or lack of fuel (high-aridity extreme) (Pausas and Bradstock 2007; Krawchuk and Moritz 2011; Pausas and Ribeiro 2013). Moreover, this relationship may be modulated by characteristics of the vegetation, making the flammability threshold of a given ecosystem context dependent (Cochrane 2003; Archibald et al. 2009; Parisien and Moritz 2009; Bradstock 2010; Pausas and Paula 2012). However, few studies have been able to broaden the spatial scale (*e.g.*, from regional to continental) to allow us to understand the potential of the climate–vegetation–fire system dynamics as a modulator of ecosystem response to fire (Archibald et al. 2013, 2018; Lehmann et al. 2014; Pausas and Ribeiro 2017).

Fire-prone ecosystems, many of which occupy the intermediate range of the productivity–aridity gradient,

feature flammable seasonal forests, grasslands, and shrublands (Bond et al. 2005), where most of the species have life-history traits that allow them to cope with fire (Bond and Keeley 2005; Keeley et al. 2011; Bond and Van Wilgen 2012; Pausas and Keeley 2014). In these environments, fire is expected to have a mild impact, and ecosystem properties are expected to return to the pre-fire state in the short term. On the contrary, in non-fire-prone ecosystems where climate maintains a high level of moisture throughout the year (*e.g.*, tropical forest), or limits biomass productivity, generating a patchy configuration of vegetation (*e.g.*, desert), most species do not have life-history traits to cope with fires or they are less efficient at coping than species in fire-prone ecosystems. Consequently, even though climatic conditions in some of these regions might lead to high productivity, and hence expected rapid biomass recovery (*e.g.*, humid tropical regions), fires usually have higher and longer-lasting negative impacts on their ecosystem properties (Gerwing 2002; Cochrane 2003; Barlow and Peres 2008; Mestre et al. 2013; Silveira et al. 2016). Moreover, in non-fire-prone systems in which climate restricts productivity, and hence biomass recovery either by low temperature or precipitation, a slow recovery after fire might be expected (Casady and Marsh 2010; Nelson et al. 2014). Therefore, the effect of fire at a broad scale, measured through biophysical variables such as biodiversity, abundance, fitness (*e.g.*, vegetative, reproductive), and soil properties (*e.g.*, bulk density, organic matter, nutrients), is expected to differ across regions with different climates (Moretti et al. 2009; Miller et al. 2013; Lehmann et al. 2014).

Fire is a discrete disturbance in time and space; thus, as post-fire succession advances, different responses may occur in the same ecosystem (Chapin III et al. 2011; Mestre et al. 2013; Cohn et al. 2015). For example, post-fire recovery of woody ecosystems has resulted in increased plant diversity soon after fire due to an increase in grasses and annual plant diversity, followed by a reduction in biodiversity as woody cover increases over time (Giorgis et al. 2013; Maestre et al. 2016; Doherty et al. 2017). Similarly, the release of nutrients, the availability of light, and the temporary decrease of competition usually associated with the post-fire environments can maximize plant fitness of fast-growing and small-sized species (*e.g.*, grasses and forbs) shortly after fire, which then decline as the forest canopy recovers (Keeley et al. 2005; Rostagno et al. 2006; Chapin III et al. 2011; Kunst et al. 2015; Pilon et al. 2021). Along the same lines, increased soil nutrient pulses that occur immediately after fire might drop after some time due to soil erosion (Certini 2005). Furthermore, abundance of certain animals (*i.e.*, invertebrates or vertebrates) could increase shortly after fire, as some species

take refuge during fire and then recolonize recently burned patches covered by grasses and forbs, while others could be positively associated with patches in later stages of post-fire succession where woody and understory plants have recovered (Robinson et al. 2013; Doherty et al. 2017; Pausas 2019). Therefore, fires might generate windows of opportunity for growth during which different species are at an optimum at different times after fire occurrence (Miller et al. 2013; Farnsworth et al. 2014; Cohn et al. 2015; Pausas and Ribeiro 2017), making time since fire a relevant variable for assessing post-fire dynamics (Whelan et al. 2002; Murphy and Russell-Smith 2010; McLauchlan et al. 2020). Since most studies are limited in time, a comparative synthetic approach of individual studies conducted at different times after fire occurrence would allow assessing changes over time.

South America holds one of the highest annual average numbers of fires worldwide (Andela et al. 2017). Most fires on this continent have an anthropogenic origin (Bowman et al. 2009), and occur in the tropics (mainly confined to northeast Brazil; Dwyer et al. 2000) during late winter and spring (Di Bella et al. 2006). Given the great climatic variability within this continent (*i.e.*, from arid to humid, and from cold to warm), we expect to find important different fire responses across ecosystems and organisms. Although fires are highly relevant for the dynamics of South American ecosystems, knowledge of their ecological impact on ecosystem attributes and processes is scarce with respect to other fire-prone areas of the world (Prichard et al. 2017; Geary et al. 2019). Here we present the first systematic review of fire responses of ecosystem and organism attributes across South America. Our study aims to provide general patterns of fire effects at the continental scale and improve our understanding of the main factors controlling post-disturbance dynamics at this scale (*i.e.*, climate and time since fire). To that end, we performed a systematic review and hierarchical meta-analysis of the existing literature of fire studies in South America to address three major questions: (1) What fire effects have been studied across South America? (2) What are the overall responses of biodiversity, abundance, fitness, and soil properties to fires? (3) How does climate and time since fire modulate those responses? Finally, we give some recommendations for future research that may help improve our understanding of fire effects in South America and the world.

Methods

Literature search and compilation of dataset

We searched for peer-reviewed publications of fire effects in South America in Scopus scientific literature database. Relevant search terms were combined into one

search string, which we used to select the titles, abstracts, and keywords of all articles in relevant areas, namely agricultural and biological sciences, environmental sciences, and earth and planetary sciences. We used the following search string:

```
(
  *fire* OR burn*
) AND (
  "South americ*" OR chile* OR argentin* OR bolivi* OR peru* OR
  brazil* OR ecuado* OR paragu* OR urugu* OR venez* OR colombi*
  OR guia* OR surin* OR "french gui*"
) AND (
  biodiversity OR abundance OR fitness OR biomass OR soil OR
  vegetation OR savanna* OR shrub* OR tree OR grass* OR *forest*
  OR wood* OR forb OR herb*
) AND (
  LIMIT-TO (SUBJAREA, "AGRI") OR LIMIT-TO (SUBJAREA, "ENVI") OR
  LIMIT-TO (SUBJAREA, "EARTH")
)
```

This search delivered 4535 studies (10 December 2019), of which we assessed their titles and abstracts, retaining 435 for a further detailed full-text check, from which we kept 160 studies. These studies were analyzed in full and all relevant data was extracted for the subsequent meta-analysis. We included articles in English, Spanish, and Portuguese. We only included articles that provided numerical parameters of the response variables of interest to compute the effect sizes, the common metric to conduct a meta-analysis, in paired burned (*i.e.*, treatment) and unburned (*i.e.*, control) plots, the latter with at least 20 years since the last fire; and that reported the time since the last fire. We did not include studies that used experimental heat treatments, or studies with confounding factors such as slash and burn practices or with obvious differences in conditions (*e.g.*, topographic position, grazing pressure) between plots (Additional file 1: Figure 1.1).

Response variables considered in the analyses

We analyzed the impact of fire on four response variables: biodiversity, abundance, fitness, and soil properties. Biodiversity and abundance were analyzed according to two levels of disaggregation. The first level included plants, fungi, invertebrates, and vertebrates; while the second level included growth forms for plants (forbs, grasses, shrubs, and trees), taxonomic order for invertebrates (*e.g.*,

Araneae, Coleoptera, Collembola, Formicidae, Orthoptera), and taxonomic class for vertebrates (birds, mammals, reptiles, amphibians). Biodiversity was mostly measured as richness (number of species) and only a few studies used other diversity indices. Abundance was mainly reported as cover percentage, biomass (for plant species), or individual number (for trees and animals). Fitness was considered as any trait of the individuals directly or indirectly related to their performance (Violle et al. 2007). As almost all of the studies assessing fire effects on fitness were conducted on plants (98%), we analyzed their vegetative (*e.g.*, specific leaf area, growth rate) and reproductive (*e.g.*, number of flowers per branch, fruit-set) fitness (Violle et al. 2007). Finally, we analyzed each soil property independently (bulk density, litter, organic matter, available nitrogen, total nitrogen, phosphorous, micronutrients, pH, and salinity). For simplicity, all the variables subjected to analysis of fire responses will hereafter be referred to as response variables.

To analyze how climate modulates the effect of fire on response variables, we classified each study site based on the relation between precipitation and temperature proposed by Whittaker (1975) for the ordination of world ecosystems. To do that, we first obtained the mean annual precipitation and the mean annual temperature of each study site from Worldclim (www.worldclim.org; Hijmans et al. 2005). The location of each study site was geo-referenced in decimal degrees and data were extracted using the `extract` function from the `raster` packages in R version 3.4.0 (R Core Team 2019) from bioclimatic data at a scale of 2.5 arcmin. If an article had several study sites (with pairs of burned and unburned plots) separated by more than 15 km, we extracted different bioclimatic data for each pair of sites and, thus, we obtained data for 175 study sites from the 160 selected articles. Secondly, based on the formula proposed by Bond et al. (2005), which follows the precipitation–temperature plane of Whittaker (1975) to define uncertain ecosystems, we classified each study site into one of the following four climate types: semiarid, dry, cold-humid, and warm-humid climates. Values of MAP (mean annual precipitation) and MAT (mean annual temperature) were used in combination with unitless constant values to define climate types (Table 1).

Humid climate was further divided into two types—humid-cold and humid-warm—depending on whether

Table 1 Formulas used to classify each study site, from studies that were published between 1990 and 2019 that were used in the review of fire effects across South American ecosystems to determine the role of climate and time since fire, into different climate types. MAP = Mean Annual Precipitation; MAT = Mean Annual Temperature

Climate types	Formulas
Humid	$\text{MAP} > 7.143 \text{ MAT} + 286$ and $\text{MAP} > -1.469 \text{ MAT}^2 + 81.665 \text{ MAT} + 475$
Semiarid	$\text{MAP} > 7.143 \text{ MAT} + 286$ and $\text{MAP} < -1.469 \text{ MAT}^2 + 81.665 \text{ MAT} + 475$
Dry	$\text{MAP} < 7.143 \text{ MAT} + 286$ and $\text{MAP} < -1.469 \text{ MAT}^2 + 81.665 \text{ MAT} + 475$

the mean annual temperature of the study sites was lower or higher than 15 °C, respectively (Additional file 2). Regarding fire proneness, there is no standardized and unequivocal way to classify the analyzed studies as fire-prone or non-fire-prone; instead, we relied on the above climate-type classifications and discuss fire proneness when it was relevant.

The time since the last fire event at which the post-fire response was measured was classified as either early (between 1 to 36 months) or late (more than 37 months). Regrettably, there were not enough studies reporting the fire frequency (19% of the studies) or the intensity or severity (2.5% of the studies) of the fire, so we were unable to include and analyze these two aspects of the fire regime.

Meta-analysis

We used Hedges' d as an estimate of the unbiased standardized mean difference (*i.e.*, the effect size) between the response variables in burned and unburned conditions, which has the advantage of being unbiased by small sample size (Gurevitch et al. 2001). To calculate Hedges' d , we extracted the mean, standard deviation, and sample size values of the response variables in burned and unburned conditions from each study. These data were extracted directly from the text, tables, or from graphs using Data Thief III software (Tummers 2006; <http://www.datathief.org/>). When some data was missing or not available, we requested it from the corresponding authors. A positive d value indicates that the response variable increases in the burned plot, whereas a negative d value implies the opposite, a decrease of the response variable in burned conditions. Hedges' d calculations were performed using the `escalc` function from `metafor` package in the software R.

We performed hierarchical mixed effects meta-analyses using the `rma.mv` function from `metafor` package in R. These mixed models were used with fixed and random effects to account for differences across studies, assuming that they do not share a common mean effect but that there is random variation among studies, in addition to within-study sampling variation (Borenstein et al. 2009). In a meta-analytical framework, when more than one effect size is obtained from the same publication, it implies pseudoreplication, violating the assumption that effect sizes are independent (Gurevitch and Hedges 1999; Tuck et al. 2014). To control for this potential source of non-independence among effect sizes, we included the identity of each study as a random factor to incorporate their hierarchical dependence when multiple observations (*i.e.*, effect sizes) were obtained from the same study (Borenstein et al. 2010; Nakagawa and Santos 2012; see models in Additional file 3: Tables 3.1 and 3.2).

Separate meta-analyses for each response variable (*i.e.*, biodiversity, abundance, plant fitness, and soil properties)

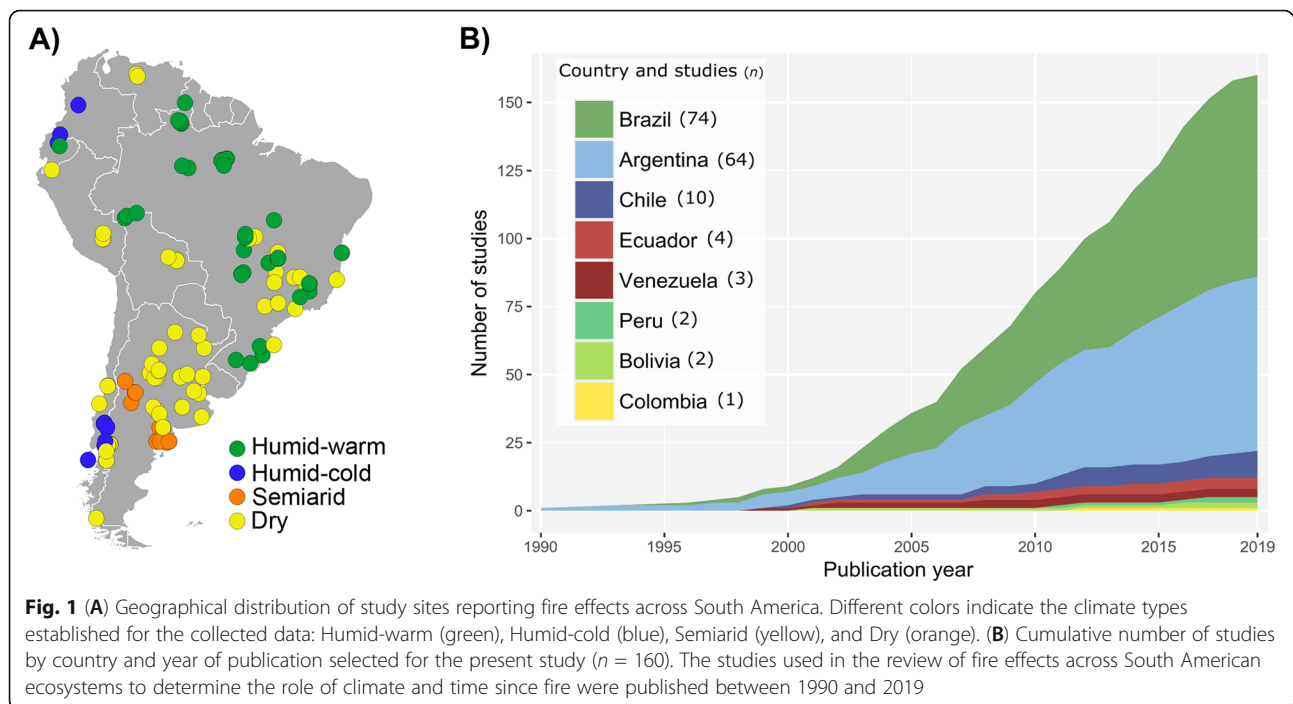
were performed using different categorical moderator variables to analyze descriptive patterns (*e.g.*, taxa groups, plant life form, etc.) or to assess whether they affect the magnitude of fire impacts (post-fire time, climate type). We also tested combinations between these moderators when the sample size allowed.

For each response variable, we tested the heterogeneity of effect sizes using Q statistics, which are weighted sums of squares tested against a chi-square distribution (Hedges and Olkin 2014). Specifically, we examined the P -values of Q -between (Q_b) statistics that describe the variation in effect sizes that can be attributed to differences among categories of each moderator variable. Effect sizes were considered significantly different from zero if their 95% bias-corrected bootstrap confidence intervals (CI) did not include zero (Borenstein et al. 2009). A common problem of any systematic review is the potential inclusion of studies that only show significant results, as they may have a greater possibility of being published than those showing non-significant results (*i.e.*, publication bias). To detect the existence of publication bias in our dataset and to estimate how such bias, if it existed, may affect the overall results, we used statistical (rank correlation tests and "trim and fill" procedures), and numerical (Rosengberg's fail-safe number) methods (Jennions et al. 2013).

Results

What fire effects have been studied in South America?

A total of 160 articles with 1465 fire responses (effect sizes) were included in our review (Additional file 1). Published articles in South America increased exponentially over the years (Fig. 1). Most of the studies in the articles were performed in Brazil (74 studies) and Argentina (64), followed by Chile (10). The remaining South American countries each had four articles or less (Fig. 1). Among all the considered response variables, fire effects on abundance had the highest number of records (544 effect sizes), followed by plant fitness, soil properties, and biodiversity (434, 354, and 133 effect sizes, respectively). Among taxonomic groups, plants had the highest number of records, focusing on plant abundance and fitness, while the responses reported for the abundance of invertebrates and vertebrates were much less frequent (Fig. 2A). Among plant growth forms, trees were responsible for most of the abundance responses, while shrubs had the majority of the fitness responses (Fig. 2B). Formicidae was the most studied order within invertebrates, while birds were responsible for most of the studies on vertebrates (Additional file 3: Table 3.2). Most of the studies were performed in semi-arid and humid warm climates (Fig. 2C). However, in humid-warm climate, studies often focused on abundance responses, while in semiarid climate, fitness responses



were more common (Fig. 2C). Early post-fire responses (<36 months) were evaluated in most of the studies, while less than half of the responses focused on late post-fire responses (>36 months; Fig. 2D). Studies including soil properties mostly focused on organic matter followed by total nitrogen, phosphorus, and pH, while few registered effects of other soil characteristics (Fig. 2E). Furthermore, most of these variables were studied in semiarid areas (Fig. 2E) and in early post fire (Fig. 2F).

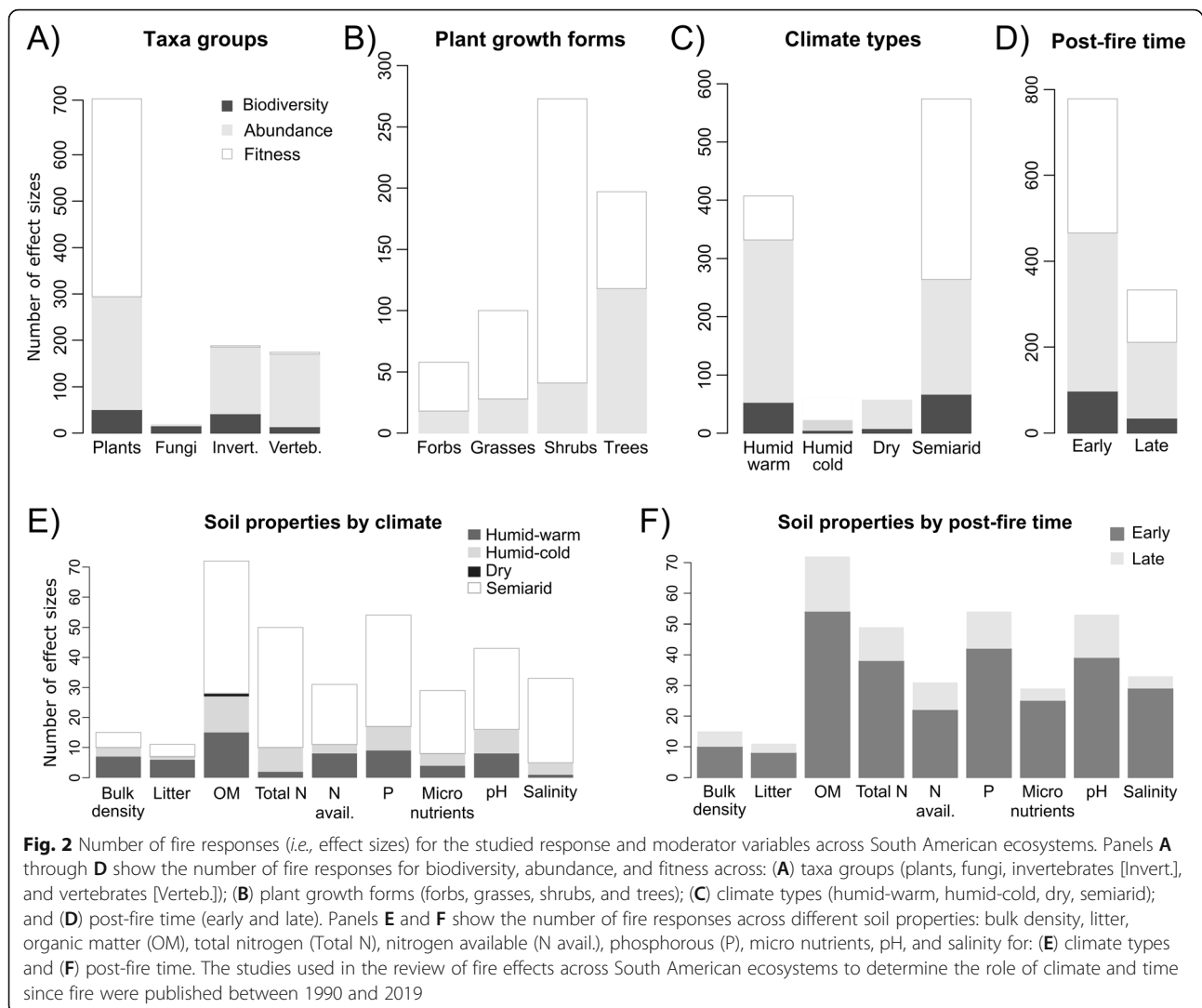
Fire responses and effects of climate and time since fire

We did not find significant effects of fire on overall biodiversity (Fig. 3; Additional file 3: Table 3.2). Similarly, no significant fire effects were observed for any of the four different broad taxonomic groups analyzed (plants, fungi, invertebrates, and vertebrates; Fig. 3; Additional file 3: Table 3.2). Moreover, biodiversity was not affected by fire across the two climates that allowed for analysis (humid-warm and semiarid), nor was it affected at different post-fire times, or when only plants were considered (Fig. 3; Additional file 3: Table 3.2).

Fire had significantly different effects on the abundance of plants, invertebrates, and vertebrates (Fig. 4). Furthermore, fire effect on overall abundance was negative for three of the four climates analyzed, with the highest negative effect occurring in dry climates, although no significant differences between climates were found (Fig. 4). Additionally, fire had a similar negative effect on overall abundance both at early and late post-fire times (Fig. 4).

For plant abundance, fire had an overall significantly negative effect (Fig. 4), which showed the same trend at both post-fire times (Fig. 5A). The negative trend persisted when the different growth forms were analyzed separately (Fig. 4; Additional file 3: Table 3.2). Specifically, this response was significant in trees and shrubs, while the abundance of forbs and grasses had similar negative but non-significant fire effects (Fig. 4). This response pattern for different plant growth forms was equal at both post-fire times (Fig. 5B). The fire response among different taxa of invertebrates showed an overall slight, non-significant, negative trend, although Orthoptera was the only order that tended to increase in abundance in response to fire (Fig. 4). Regarding vertebrates, overall abundance decreased in burned conditions, mostly driven by the negative effect on birds, while mammals, reptiles, and amphibians were not significantly affected by fire (Fig. 4, Additional file 3: Table 3.2). Vertebrate abundance decreased, on average, in early post-fire scenarios but showed no effect in late post fire, indicating some level of recovery along post-fire succession, although the differences between times were not statistically significant (Fig. 5A). Except for invertebrates, abundance responses of shrubs, trees, and vertebrates showed similar trends across the analyzed climate types (Fig. 5C).

We found significantly different fire effects on plant fitness among different plant growth forms, and between early and late post-fire times (Fig. 6A; Additional file 3: Table 3.2). Fire produced an increase on vegetative and reproductive shrub fitness, which was particularly



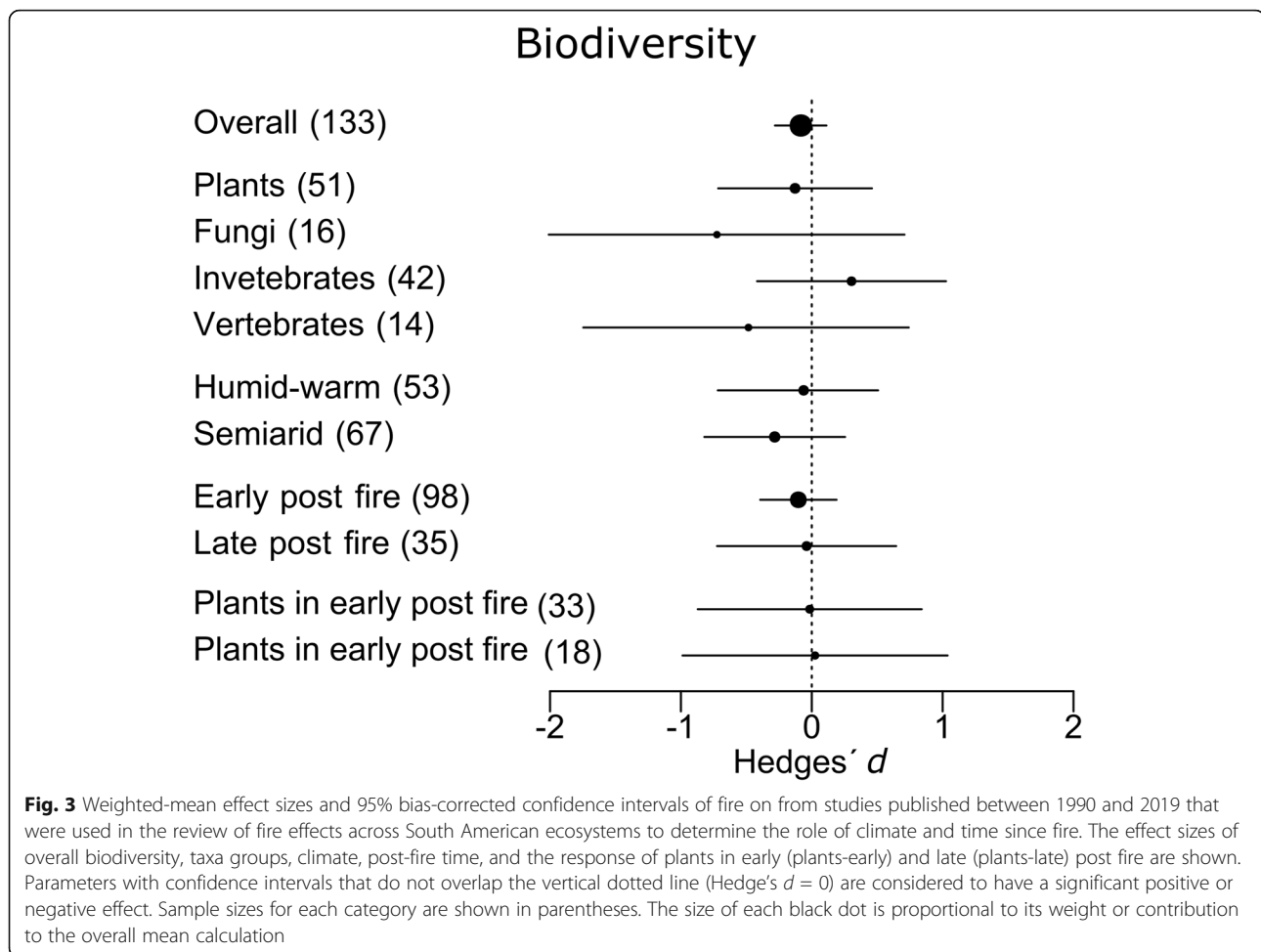
evident early post fire (Fig. 6B, C). Grasses showed a significant negative response to fire in vegetative fitness only during early post-fire, while fire effect had a positive trend on reproductive performance (Fig. 6B, C). Forbs and trees showed an overall non-significant fire effect on their fitness (Fig. 6A, B, C). However, a trend toward positive fire effects of the vegetative fitness of trees early post fire was observed (Fig. 6C).

Regarding soil properties, in burned we found plots reductions in litter, OM, total nitrogen and available nitrogen, and increases in bulk density and pH (Fig. 7A; Additional file 3: Table 3.2). Additionally, we found enrichment of phosphorus early post fire, which differed significantly from late post fire (Fig. 7B). The reduction in organic matter and total nitrogen in burned plots was mainly driven by their response early post fire and in semiarid climates, while for available nitrogen, it was more notable late post fire (Fig. 7B). Increasing values in

pH mainly occurred early post fire and in semiarid climates (Fig. 7B; Additional file 3: Table 3.2).

Publication bias

We found no evidence of publication bias for the meta-analyses of fire effects on abundance and biodiversity, as observed by the lack of correlation between sample size and effect sizes. Furthermore, we found no changes in overall effect sizes in the “trim and fill” procedures (Additional file 4: Table 4.1). In contrast, for the meta-analyses of fire effects on plant fitness and soil properties, we found low but significant correlations between effect sizes and sample sizes, indicating the potential presence of publication bias (Additional file 4: Table 4.1). However, the “trim and fill” methods only slightly changed the overall results for each of these meta-analyses. Moreover, all of the calculated weighted fail-safe numbers were always larger than the threshold



number of $5n+10$ (where n is the number of studies included in the meta-analysis), implying that the results found in our review were robust regardless of the presence of publication bias (Additional file 4: Table 4.1).

Discussion

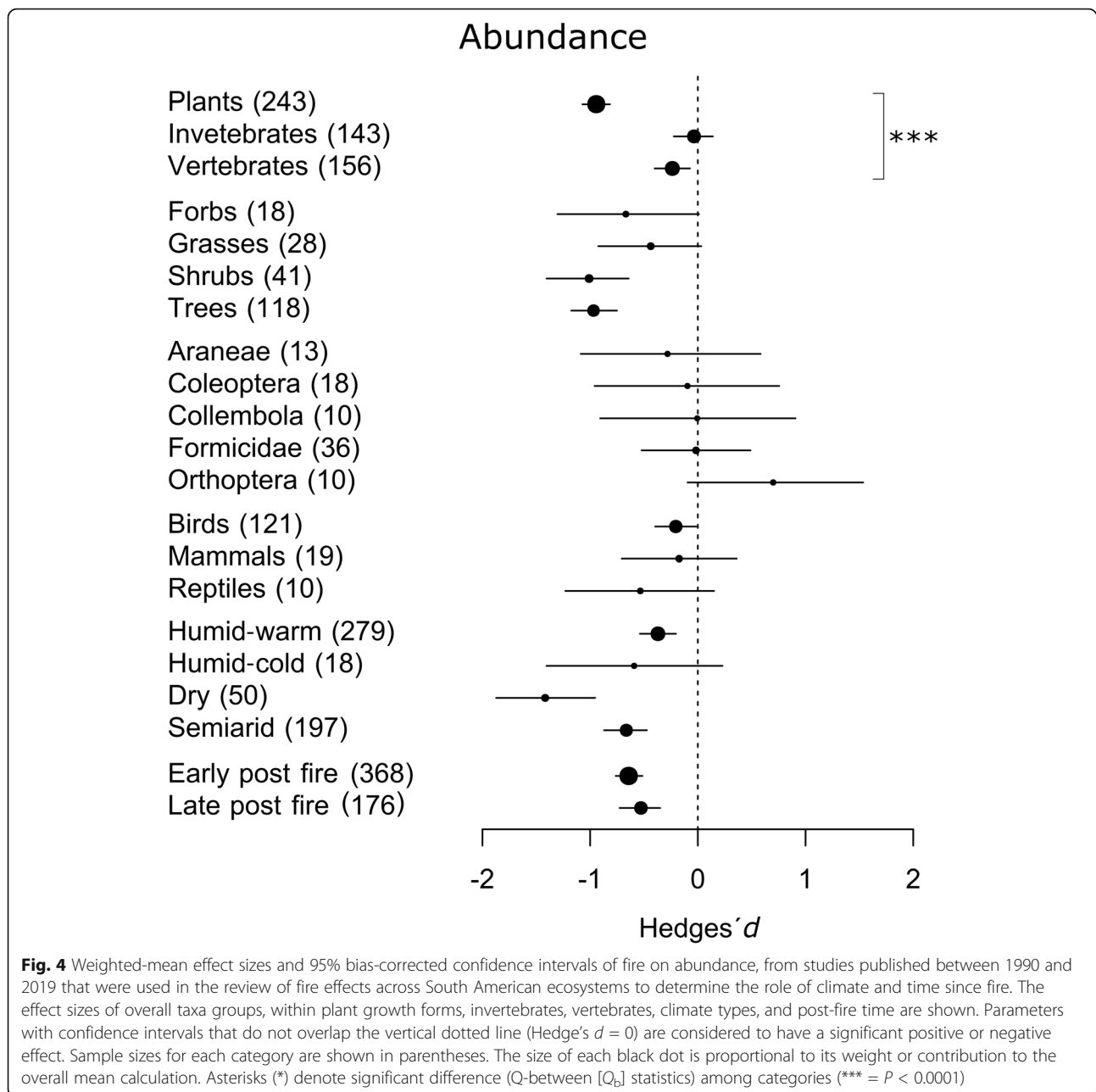
This is the first systematic quantitative review assessing fire effects on multiple taxonomic groups across different climate types and post-fire times in South America, one of the world's most burned continents. Our results show non-significant effects of fire on biodiversity, a sharp negative effect on abundance of woody plant and vertebrate species, and an increase in plant fitness of shrubs. In addition, we observed clear negative fire effects in the most important soil properties as was previously found at a global scale. Our meta-analysis showed a tendency of stronger negative effect in semi-arid climate than in tropical warm climate, indicating that higher temperatures and water availability in the latter climate allow a faster ecosystem recovery after fire. Additionally, more significant fire effects were observed

early post fire than late post fire, indicating stronger effects immediately after fire and their dilution over time.

Effect of fire on the response variables

Biodiversity. Biodiversity was not significantly affected by fire across any taxa group, climate type, or time since fire, indicating an overall high resilience at the analyzed spatial and temporal scales. This is in line with previous studies focused on specific semi-arid regions, including two well-studied large fire-prone ecosystems in South America (*i.e.*, Cerrado and the Gran Chaco), which had shown post-fire recovery of biodiversity for different taxa groups, such as plants, birds, and insects (*e.g.*, Kunst et al. 2003, 2015; Kowaljew et al. 2019; Durigan et al. 2020; Pilon et al. 2021). However, these responses may certainly involve context-dependent changes in species composition (Durigan et al. 2020; McLauchlan et al. 2020), which could not be captured in our quantitative synthesis.

Interestingly, we found a tendency toward higher invertebrate biodiversity in burned plots compared to controls. This pattern has been reported in different areas around the world (*e.g.*, (Knoechelmann and Morais



2008; Uehara-Prado et al. 2010; Carbone et al. 2019; Lazarina et al. 2019), and could be explained by the high mobility of many invertebrates (e.g., arthropods), which can take advantage of the usually high availability of plant biomass in early post-fire succession (Miranda et al. 2002; Hoffmann and Andersen 2003). Contrary to invertebrates, diversity of fungi (i.e., mycorrhizas) tended to decrease (Fig. 3), probably as a response to the globally general negative effect of fire on soil microbial communities (Pressler et al. 2019) and soil quality (Certini 2005; Pellegrini et al. 2018). However, fungi and vertebrates are groups that deserve further study, given the

spatial and temporal scarcity of fire effects studies on these organisms. Currently, fungi research is highly restricted geographically (all studies from Argentina; Longo et al. 2011, 2014), while vertebrates showed the lowest number of studies, even though this group is fundamental for controlling cascading effects across trophic levels (Bruno and Cardinale 2008; Cavallero et al. 2013; Kurten 2013; Bauer and Hoye 2014; Dirzo et al. 2014; Pérez-Méndez et al. 2016).

Abundance. As expected, fire negatively affected plant abundance, mainly driven by the impact on woody species (i.e., shrubs and trees). The negative impact on these

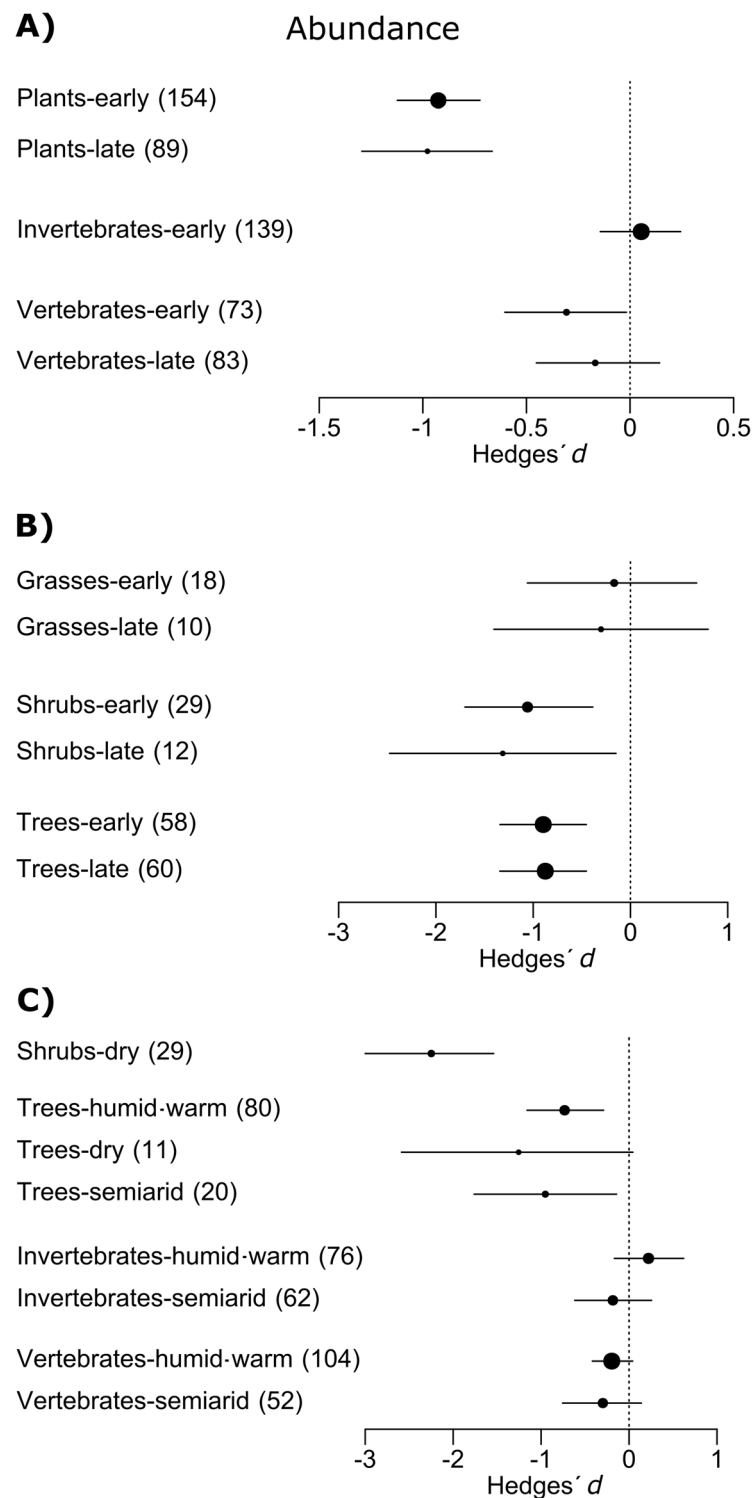
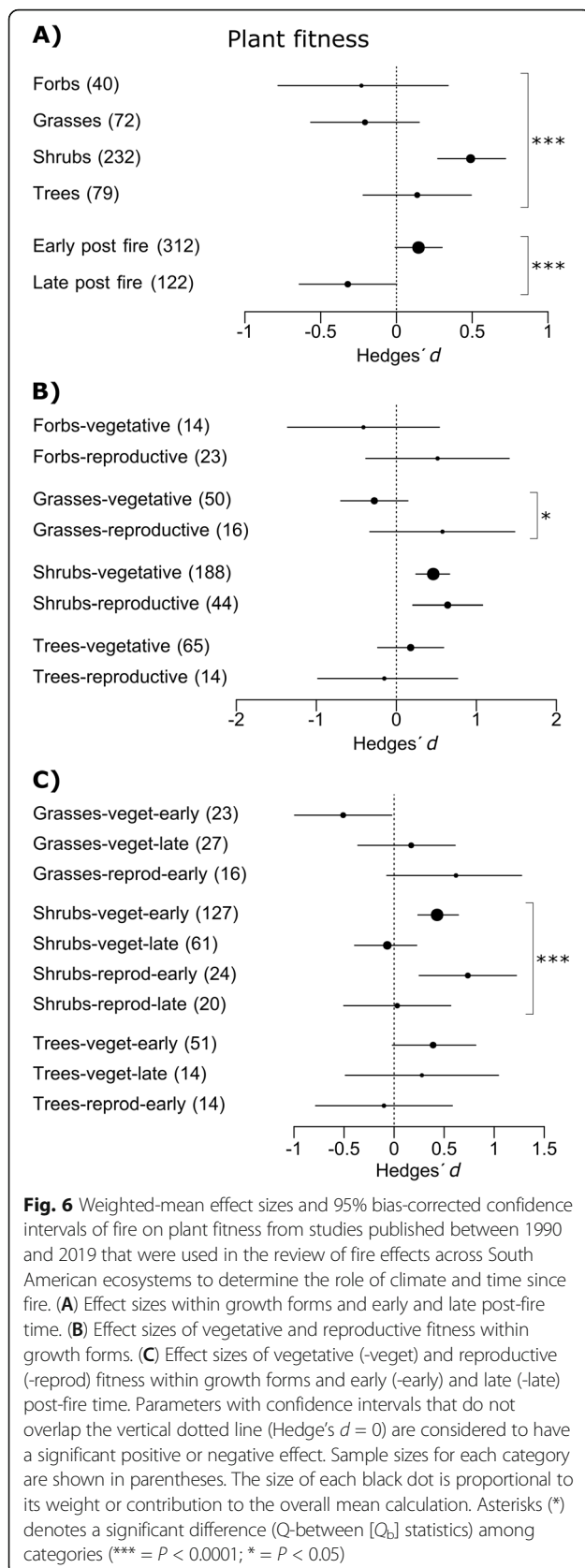


Fig. 5 Weighted-mean effect sizes and 95% bias-corrected confidence intervals of fire on abundance from studies published between 1990 and 2019 that were used in the review of fire effects across South American ecosystems to determine the role of climate and time since fire. The effect sizes of early (-early) and late (-late) post-fire time for abundance of **(A)** plants, invertebrates, and vertebrates; and **(B)** grasses, shrubs, and trees. **(C)** The effect sizes of shrubs, trees, invertebrates, and vertebrates across different climate types (-dry, -semiarid, -humid-warm). Parameters with confidence intervals that do not overlap the vertical dotted line (Hedge's $d = 0$) are considered to have a significant positive or negative effect. Sample sizes for each category are shown in parentheses. The size of each black dot is proportional to its weight or contribution to the overall mean calculation. None of the effect sizes of the groups within each moderator variable are significantly different (see Additional file 3: Table 3.2 for heterogeneity tests)



growth forms early and late post fire (Fig. 5B) is expected considering that the relative recovery of pre-fire abundance (including cover and biomass) is slower than in herbaceous species. The strongest negative effect observed for shrubs could be mainly due to the fact that most of the studies were carried out in dry-climate ecosystems, where the combination of water stress and fire significantly limits shrub recovery (Casillo et al. 2012; Pratt et al. 2014; Jacobsen et al. 2016).

After fire, a combination of different processes may limit woody species recovery. First, woody species in non-fire-prone ecosystems may experience high mortality rates (Barlow et al. 2003). Second, the reduction in aboveground biomass produced by fires exposes individuals to direct influence of browsing and trampling by livestock (Coop et al. 2010; Blackhall et al. 2015, 2017; Marcora et al. 2018; O'Connor et al. 2020; Zeballos et al. 2020). Third, recruitment of woody species seedlings into fire-promoted grasslands or herbaceous patches may be more restricted due to an increase in competition for light, water, or nutrients (Scholes and Archer 1997; Casillo et al. 2012). Finally, soil erosion driven by fire increases run-off and seed loss events, and reduces nutrient availability, therefore constraining biomass production (Silva et al. 2013; Balch et al. 2015). The lesser negative effect observed in forbs and grasses may be attributed to their relative higher growth rate and shorter lifespan as compared to woody species, which result in a faster recovery in burned habitats. This vegetative response might be linked to the responses observed in some of the mobile organisms (Fig. 4). For example, the early recovery of herbaceous vegetation could promote rapid re-colonization by invertebrates such as insect herbivores and pollinators. Additionally, our results indicated different trends of abundance recovery across taxa groups of invertebrates and vertebrates. Similarly, a previous review showed different patterns of "optimum" abundance as time since fire increased (Doherty et al. 2017). The fast recovery of invertebrate abundance early post fire was mainly driven by insect studies (Carbone et al. 2019), particularly on Orthoptera (Silveira et al. 2010; Kral et al. 2017). In turn, the overall negative effect of fire on the abundance of vertebrates was mainly driven by bird studies, which mostly showed a negative response to fire (Fig. 5). Although this pattern has been observed in other ecosystems (Fontaine and Kennedy 2012; Doherty et al. 2017; Carbone et al. 2019), the response of birds to fire can be heterogeneous, varying considerably between taxonomic and functional groups (Fontaine and Kennedy 2012); therefore, generalizations may be difficult to establish. The pattern observed here could be due to the fact that the systematically selected studies focused on rather intense fires, or on bird species that are more susceptible to fire. Our findings of some

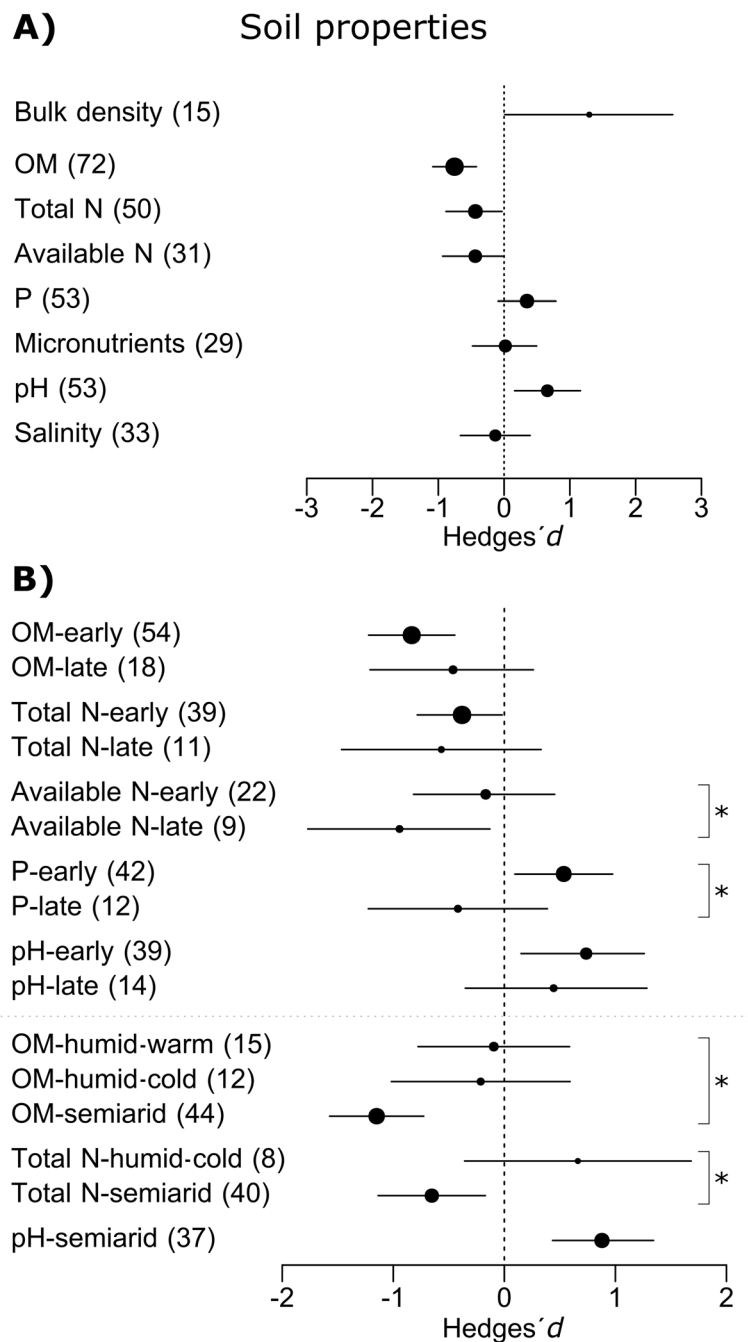


Fig. 7 Weighted-mean effect sizes and 95% bias-corrected confidence intervals of fire on soil properties from studies published between 1990 and 2019 that were used in the review of fire effects across South American ecosystems to determine the role of climate and time since fire. **(A)** Effect sizes of bulk density, litter, organic matter (OM), total nitrogen (Total N), available nitrogen (N), phosphorous (P), micronutrients, pH, and salinity are shown. **(B)** Effect sizes of early (-early) and late (-late) post-fire time of organic matter, total nitrogen, available nitrogen, phosphorous, and within climate type (-humid-warm, -humid-cold, -semiarid) of organic matter and total nitrogen. Parameters with confidence intervals that do not overlap the vertical dotted line (Hedge's $d = 0$) are considered to have a significant positive or negative effect. Sample sizes for each category are shown in parentheses. The size of each black dot is proportional to its weight or contribution to the overall mean calculation. Asterisk (*) denotes a significant difference (Q-between [Q_b] statistics) among categories (* = $P < 0.05$)

level of recovery of vertebrate abundance late post fire compared to early post fire (Fig. 5) could have been driven by the re-establishment of some bird populations

over time (Fontaine and Kennedy 2012; Doherty et al. 2017). Additionally, the recovery of populations of specialist birds may take longer, particularly in forest

ecosystems (e.g., Barlow and Peres 2004; Fontaine and Kennedy 2012; Mestre et al. 2013; Albanesi et al. 2014), although there are exceptions (e.g., Fontaine and Kennedy 2012; Lee 2018; Morales et al. 2020), such as the group of birds known as cavity excavators (i.e., woodpeckers [Picidae]), that take advantage of both the softness of the wood of recently burned trees (i.e., snags) for making their cavities (Schepps et al. 1999; Winkler and Christie 2002; Bond et al. 2012; Lorenz et al. 2015) and the higher amount of food (insect and other invertebrates) found in that substrate right after the fire (Murphy and Lehnhausen 1998; Nappi et al. 2003).

Plant fitness. Despite the negative effect of fire on tree abundance, we found no effect of fire on tree fitness, and a slight positive trend on vegetative fitness early post fire (Fig. 6A, B). Many tree species in the analyzed ecosystems are highly resilient to individual fires, mainly through resprouting (Hoffmann and Solbrig 2003; Soucie et al. 2017; Jaureguiberry et al. 2020); therefore, if burned plots do not burn again, trees might grow and recover their biomass (Doherty et al. 2017; Miller et al. 2019; Coop et al. 2020). This response does not necessarily imply a direct adaptation to fire, as the fire-adaptive traits on which it relies could also have arisen in response to other factors that have had a long history in some of the studied regions, such as herbivory and seasonal drought (Keeley et al. 2011), which indirectly provide the vegetation with a high resilience to fire. On the other hand, the negative tendency of the reproductive fitness observed early post fire is expected, since trees may take a long time to recover their reproductive size (Chapin III et al. 2011). In contrast to trees, shrubs did show an increase in vegetative and reproductive fitness early post fire, which differs significantly from that of late post fire (Fig. 6C). The early vegetative response reflects the high resprouting capacity of many shrub species across the studied regions, especially in fire-prone regions (Gurvich et al. 2005; Bravo et al. 2014; Torres et al. 2014; Durigan et al. 2020; Jaureguiberry et al. 2020). Regarding the reproductive response, the pattern reported here agrees with previous evidence suggesting that shrubs might reach minimum reproductive sizes soon after fire, then slow down their growth rate and reproduction as succession progresses (Hoffmann and Moreira 2002; Hoffmann and Solbrig 2003; Galíndez et al. 2009). In the case of herbaceous plants, surprisingly we did not find a general effect in fitness, but a positive trend in reproductive fitness was observed, mainly early post fire for grasses (Fig. 6B, C). The lack of a consistent general response pattern in forbs could be explained by the high heterogeneity of functional groups included within this growth form (e.g., annual, perennial, climber, fern) that can have different responses to fire (Keeley et al. 1981; Bates et al. 2014; Heydari et al. 2016; Arcamone and Jaureguiberry 2018; Vidaller et al.

2019). In the case of grasses, the tendency of increasing reproductive fitness early post fire (Fig. 6C) could be related to the positive fire–colonization feedback generally described for this growth form (Bond et al. 2003; Bond and Keeley 2005; Pausas and Keeley 2009; Pilon et al. 2018). Previous studies had observed an increase in reproductive fitness of grasses after fire (Baruch and Bilbao 1999; Araújo et al. 2013; Pilon et al. 2018; Vidaller et al. 2019). On the contrary, vegetative fitness showed a negative impact early post fire. However, we cannot determine if the observed pattern (i.e., positive reproductive fitness versus negative vegetative fitness) was due to intrinsic differences between types of fitness or to differences in the type of climate, since all studies on reproductive fitness were located in humid-warm climate, while vegetative fitness was mostly studied in semiarid and arid climates.

Soil properties. The responses of soil properties to fire in South American ecosystems support the trend suggested in previous global reviews (Certini 2005; Pellegrini et al. 2018). Fire significantly reduces the amount of two important soil properties: OM and nitrogen content (Pellegrini et al. 2018). On the one hand, OM is directly associated with carbon concentration in the soil, one of the most stable carbon reservoirs worldwide, thus large-scale losses of OM due to fire could have important implications for global climate change (Lal 2004). On the other hand, nitrogen is often the most limiting soil nutrient for plant growth and its loss directly affects ecosystems by reducing net primary productivity (Vitousek and Howarth 1991; Pellegrini et al. 2018). In addition, our results of a higher negative effect of fire on OM in semiarid climates compared to humid-warm climate is supported by Pellegrini et al. (2018), who found that across savannas and grasslands, biannual fire simulation induces high carbon losses under drier climates. However, it has been recently proposed that a single fire event may be related to either an increase, a decrease, or no change in soil carbon and nitrogen; while frequent fires over time produce a consistent decrease of both elements across ecosystems (Pellegrini et al. 2020a, b). This hypothesis poses a constraint to our analyses, since most of the articles did not report fire history for their study sites. Consequently, the heterogeneous effects of single fires on soil carbon and nitrogen may be confused with those of frequent fires, therefore limiting the identification of clearer patterns.

Fire produces an increase in bulk density as a result of soil disaggregation due to the decrease or loss of OM and to the infiltration of ashes into soil micropores (Boyer and Miller 1994; Mataix-Solera et al. 2011). Soil pH also increased in burned plots as a result of organic acid denaturation due to soil heating and the accumulation of potassium and sodium hydroxides and magnesium and calcium carbonates

(Knicker 2007). The increase in pH is also driven by the reduction in OM (Certini 2005). Additionally, immediate phosphorus enrichment after a fire event is the result of organic pool conversion of phosphorus into orthophosphate, which declines at later post-fire times, as it is also suggested by Certini (2005).

Climate–fire–vegetation feedbacks. Our review suggests that climatic conditions associated with higher rates of biomass accumulation might determine a faster ecosystem recovery in burned sites across South America. We found a faster recovery in invertebrate abundance and lower losses of soil organic matter under climates with higher water availability and temperatures than in semiarid climates. Beyond climatic conditions, in historically fire-prone ecosystems, where fire has presumably been an important evolutionary factor (Bond and Keeley 2005), a greater recovery of the biota is expected compared to non-fire-prone ecosystems. However, our classification of climate types may not necessarily reflect the fire history of the corresponding regions, therefore making a clear interpretation of the reported patterns difficult. Although semiarid climate sites could be clearly considered as fire-prone systems (Bond 2005), warm-humid climate sites may also include fire-prone ecosystems, because some of them have seasonal rainfall patterns, which is a key characteristic in determining the fire proneness of an ecosystem (Nogueira et al. 2017; Romano and Ursino 2020). In fact, following the classification of Olson et al. (2001), 40% of the studies from warm-humid areas corresponded to tropical and subtropical grassland, savanna, and shrublands biome (arguably fire prone), while the other 60% corresponded to tropical and subtropical moist broadleaf forest biome (arguably non-fire prone). Most of the former were located in the Cerrado region, where Hoffmann and Moreira (2002) found a faster post-fire recovery of woody species compared to neighboring tropical forest areas. Thus, they concluded that the combination of fire-prone vegetation, presumably with a long fire history, and warm-humid climate might favor a fast ecosystem recovery after fire. Therefore, the observed results of greater recovery in warm-humid ecosystems types is likely due to a combination of both climate and fire history. Likewise, most of the studies from cold-humid areas have a mediterranean-type climate (e.g., northwest Patagonia in Argentina; Keeley et al. 2012), where rainy winters and hot and dry summers make these regions fire prone. Such regions have been historically subjected to periodic fires (both natural and anthropogenic), and therefore many plant species are capable of recovering after a fire event (Veblen et al. 2003, 2008; Defossé et al. 2015). Interestingly, we found a significant post-fire decrease in nitrogen content and soil OM under semiarid climate, but not under cold-humid climate. This response pattern may be due to the inherent

differences in ecosystem properties between climate types (e.g., decomposition and growth rates, successional patterns, and fire regimen, among others; McLauchlan et al. 2020). Fire regime might play an important role as more frequent surface fire in semiarid ecosystems could lead to a lower recovery of soil properties compared to cold-humid ecosystems, where crown fires predominate and fire frequency is lower than in semiarid ecosystems, therefore buffering fire effects on soil properties.

The lack of a standardized classification of fire-prone and non-fire-prone regions, as well as the limited available information on the frequency, intensity, and severity of fires in the research studies included in this review, are certainly limitations that call for precaution in the interpretation and extrapolation of the results reported here. Overcoming such limitations remains a challenge in fire ecology (Harris et al. 2016; Kelly et al. 2018). We believe that our study represents a step forward in the synthesis of fire-related patterns at a large scale. Our meta-analysis, as well as the discussed patterns, provides relevant information toward understanding the feedback between climate, vegetation, and fire on the South American continent. An ultimately desirable goal in the medium or long term would be the development of a global network of fire field experimental surveys across systems with different vegetation types and fire histories.

Future perspectives

Across recently published global fire reviews, there is clearly a low representation of studies from South America (Prichard et al. 2017; Geary et al. 2019). Given the relevance of this continent in the global dynamics of fire, it is highly necessary that more studies on different aspects of fire ecology be carried out throughout fire-prone regions of the continent (e.g., seasonal forests, and humid and semiarid savannas). Furthermore, our review allowed us to identify specific research gaps, which can be added to the agenda of research priorities for future studies in fire ecology (McLauchlan et al. 2020).

Most of the analyzed studies failed to include fire characteristics such as frequency, intensity, and severity, which prevented us from obtaining a reliable pattern of their role as modulators of ecosystem and organism responses to fire. This is an unmet challenge in fire research as these fire characteristics may certainly influence the trends reported in this review (Keeley 2009; Fontaine and Kennedy 2012; Balch et al. 2015; Silveira et al. 2016; Carbone et al. 2019).

Considering that woody ecosystems might take more than 40 years to recover after fire (Cavallero et al. 2015;

Doherty et al. 2017), studies on fire responses that span a short recovery period fail to elucidate what might happen in the meantime between fire occurrence and recovery. Consequently, our review poses an urgent call to increase the studies assessing changes in fire effects over longer post-fire times than those usually considered.

Further studies focusing on biodiversity are needed to increase sensibility to detect changes across taxa groups, climate types, and post-fire times.

Additionally, there is a gap of studies on vertebrate responses to fire, and some of the few available ones have methodological limitations, which prevented us from including them in our analysis (e.g., lack of replicates in mammals studies; Griffiths and Brook 2014).

Studies dealing with fire and exotic or invasive species were quite scarce. While invasion ecology has shown increasing attention in the last decades (e.g., Gurevitch et al. 2011; Pyšek et al. 2020), it does not seem to be reflected in fire studies in South America (but see Chaneton et al. 2004; Hoffmann et al. 2004; Mazía et al. 2010; Raffaele et al. 2016; Herrero et al. 2016; Marcora et al. 2018). We believe that this should be a priority topic for future research, particularly considering the tight link between plant invasions and changes in fire regimes (Brooks et al. 2004; Mandle et al. 2011; Harris et al. 2016).

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s42408-021-00100-9>.

Additional file 1. Supplementary material regarding the choice of studies published between 1990 and 2019 that were used in the review of fire effects across South American ecosystems to determine the role of climate and time since fire. **Figure 1.1.** PRISMA flow diagram representing the flow of information through the decision process (i.e., the number of studies identified, rejected, and accepted) for the meta-analysis of fire effects across South American ecosystems, to determine the role of climate and time since fire. Studies used were published between 1990 and 2019. **List 1.1.** List of reviewed studies, published between 1990 and 2019, that were used in the meta-analysis of fire effects across South American ecosystems to determine the role of climate and time since fire.

Additional file 2. Distribution across the climatic temperature–precipitation plane of study sites ($n = 175$) from the 160 articles reviewed for the meta-analysis of fire effects across South American ecosystems to determine the role of climate and time since fire. Studies used were published between 1990 and 2019. The four climate types established for the collected data are indicated by different colors.

Additional file 3. Distribution across the climatic temperature–precipitation plane of study sites ($n = 175$) from the 160 articles reviewed for the meta-analysis of fire effects across South American ecosystems to determine the role of climate and time since fire. Studies used were published between 1990 and 2019. The four climate types established for the collected data are indicated by different colors. **Table 3.1.** Synopsis of models used in the different hierarchical mixed effects meta-analyses of fire effects across South American ecosystems, taken from studies published between 1990 and 2019, to determine the role of climate and time since fire, expressed in R language syntax, using the metafor package (Viechtbauer 2010). y_i = Hedges' d ; v_i = variance of Hedges' d . ID = effect identity. **Table 3.2.** Summary of the fire effects on biodiversity, abundance, fitness, and soil properties showing tests of moderator variables

and heterogeneities from the meta-analyses of fire effects across South American ecosystems to determine the role of climate and time since fire. Studies used were published between 1990 and 2019. Significant influence of moderators is indicated in **bold**, when $P \leq 0.05$ and the 95% confidence interval (CI) does not include zero. Non-significant effects ($P > 0.05$) are indicated with “ns.” Note that Q-total (Q_T) statistics are reported for overall effect, and Q-between (Q_b) statistics are reported for categorical moderator variables.

Additional file 4: Supplementary information 4.1. Publication bias for the meta-analysis of fire effects across South American ecosystems to determine the role of climate and time since fire. Studies used were published between 1990 and 2019. **Table 4.1.** Sample size (number of observations) and results of publication bias and hierarchical models testing for each response variable in our meta-analysis of fire effects across South American ecosystems to determine the role of climate and time since fire. Studies used were published between 1990 and 2019. Publication bias was tested using fail-safe number (i.e., Rosenberg method), Kendall's rank correlation test (τ), and “trim and fill” models.

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Authors' contributions

MAG, SRZ, LC, RA, HZ, HvW, and PJ designed the research and analyses. MAG, SRZ, LC, RA, and PJ conducted literature search with the contribution of all the authors; MAG, LC, and PJ wrote the article with contributions from RA, AF, PT, and EK. All authors read and approved the final manuscript.

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Availability of data and materials

No unique data were created in the writing of this manuscript, so no additional data are available.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Consent for publication not applicable as we use previously published.

Competing interests

The authors declare that they have no competing interests.

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