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RESEARCH ARTICLE

Soil fertility shapes fire activity across Mediterranean-type climate regions

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Abstract

Aim: To quantify the role of soil fertility in the spatial variability of fire activity and to identify the mechanisms that drive this variability.

Location: The five Mediterranean-type climate regions of the world.

Time Period: 2002–present.

Major Taxa Studied: Terrestrial plants.

Methods: We compiled remotely sensed data on fire activity, climate, net primary productivity and chemical soil properties for bioclimatically homogeneous zones within the five Mediterranean-type climate regions of the world. Putative direct and indirect effects of the environmental variables on fire activity were evaluated through structural equation modelling.

Results: Fire activity increased with net primary productivity, as expected for ecosystems with fuel-limited fire regimes. Soil acidity and the concentration of exchangeable aluminium also increased fire activity, supporting the idea that low fertility promotes plant characteristics that favour fire initiation and spread.

Main Conclusions: Our research supports a positive relationship between wildfires and low soil fertility in Mediterranean-type climate regions across the globe. Therefore, soil fertility should be incorporated into models predicting future fires in a warming world.

KEYWORDS
fire regime, fuel loading, fuel moisture, fuel quality, macroecology, plant flammability, pyrogeography, soil aluminium, soil pH

1 | INTRODUCTION

Fire is an intrinsic process of the Earth's system, with contrasting patterns of occurrence, intensity and extension in the different regions of the world (Archibald et al., 2013). Part of this variability is due to the unimodal relationship of fire activity with net primary productivity (NPP) (Pausas & Ribeiro, 2013). In arid and unproductive ecosystems, vegetation is scarce, and thus, the fire regime is fuel-limited; on the contrary, fuel is abundant in productive ecosystems, but it is often too wet to ignite and spread fires, resulting in drought-driven fire regimes. Therefore, the highest fire frequency occurs in ecosystems with intermediate productivity and high seasonality, where wet periods that favour plant growth alternate with dry periods that make the fuel flammable (Bradstock, 2010; Pausas & Ribeiro, 2013). Despite the fact that this intermediate productivity hypothesis explains an important part of the variability in fire regimes worldwide (Krawchuk & Moritz, 2011; Pausas & Ribeiro, 2013), when this global pattern is analysed in depth, it becomes clear that it is largely driven by grassy and Mediterranean ecosystems, suggesting that the fire–climate relationship is modulated by the vegetation characteristics and the underlying environmental factors (Archibald et al., 2018; Pausas & Paula, 2012).

Soil fertility has also been proposed as a driver of the spatial patterns of fires. For instance, in seasonal tropical ecosystems, non-flammable (pyrophobic) forests are often limited to fertile pockets within vast areas of unfertile soils occupied by flammable (pyrophilic) savannahs (Hoffmann et al., 2012; Kellman, 1984). Similarly, Orians and Milewski (2007) proposed that the high frequency of fires in Australia (regardless of the ecosystem-type) can be explained by the nutrient poverty of this ancient land surface. Similarly, in the Mediterranean Basin, the abundance of species with highly flammable tissues is higher in woody communities growing on acid, nutrient-poor soils than in fertile sites within the same region and climate (Ojeda et al., 2010). Although all these examples propose that the vegetation growing on unfertile soils is more flammable, there is still no rigorous evidence on how soil fertility modulates fire activity through its effect on fuels.

Soil fertility can modulate the spatial patterns of fire activity by affecting the fuel loading in different (and opposite) ways. On the one hand, the organic matter in the soil is the main source of many nutrients necessary for plant growth, particularly those nutrients that are primarily under biological control, such as nitrogen (Delgado-Baquerizo et al., 2013). In addition, organic matter increases nutrient availability to plants by (i) preventing nutrient leaching due to its high cation exchange capacity (CEC) and (ii) increasing nutrient fluxes (especially of nitrogen) by maintaining a high soil water-holding capacity (Daou & Shipley, 2019; Schroth & Sinclair, 2003). Therefore, soils rich in organic matter foster plant growth (Stevenson, 1994), increasing the amount and continuity of fuel for fire spread. On the other hand, plants growing on unfertile soils may grow slower but tend to have carbon-rich tissues with low decomposition rates (Cornwell et al., 2008; Couteaux et al., 1995), favouring the accumulation of recalcitrant dead biomass, and thus increasing the fuel loading (Cornelissen et al., 2017; Michelaki et al., 2020).

Fuel moisture depends on soil humidity (Qi et al., 2012; Rakhmatulina et al., 2021), which in turn varies with the organic matter content of the soil (Hudson, 1994). Therefore, soils poor in organic matter are expected to promote drier, and thus, more fire-prone vegetation. In addition, natural plant communities living on poor soils are more open, which prevents the humid microclimate conditions that inhibit fires (Barberá et al., 2023; Holdo & Mack, 2014). Furthermore, plants growing in unfertile soils develop traits that favour flammability by decreasing tissue moisture. For instance, these plants tend to have small leaves (McDonald et al., 2003), being more flammable than large-leaved plants (Calitz et al., 2015; Pausas et al., 2017; Pérez-Harguindeguy et al., 2016). Similarly, plants growing on unfertile soils generate leaves and twigs with high dry matter content (Hodgson et al., 2011; Yan et al., 2013) that tend to be highly flammable as they allow plants to survive with low water content (Santacruz-García et al., 2019; Saura-Mas et al., 2009; but see Mason et al., 2016 for wet ecosystems).

Soil fertility also modulates the morpho-chemical characteristics of plants, which in turn affect their intrinsic propensity to ignite and sustain flames (i.e., fuel quality or flammability). This is because plants growing in unfertile soils tend to produce high amounts of carbohydrate-rich, nutrient-poor biomass with abundant carbon-based herbivory deterrents such as high lignin/nutrient ratio, high leaf dry matter content (LDMC), low specific leaf area (SLA) or high concentration of volatile compounds as terpenes (Coley et al., 1985). These suites of traits increase flammability (Alam et al., 2020; Grootemaat et al., 2015; Mason et al., 2016; Pausas et al., 2016; Santacruz-García et al., 2019). Furthermore, for the same moisture, heating nutrient-poor fuels promotes the release of flammable volatile gases over char formation, which shortens ignition time and increases both heat release rate and flame propagation (Armstrong & Vines, 1973; Broido & Nelson, 1964; Lowden & Hull, 2013; Scarff & Westoby, 2008). This explains why phosphorous and nitrogen are recognized as fire retardants (Lowden & Hull, 2013; Scarff & Westoby, 2008).

The Mediterranean-type climate regions (MCRs) constitute a paradigmatic study system for the evaluation of the role of soil nutrients on fire activity at a regional scale since (i) the high climate seasonality provides dry fuels available for fires every year; and (ii) MCRs include a marked variability in soil fertility (Keeley et al., 2012; Pausas & Ribeiro, 2013). Here, we hypothesize that soil fertility modulates fire activity in MCRs by directly or indirectly affecting the amount, moisture and quality of fuels (and thereafter, its flammability). However, to evaluate the role of soil nutrient availability on fire occurrence, climate must also be considered, because global and regional analyses indicate that climate interacts with soil fertility to explain variability in different plant traits, as small leaf, high LDMC and low SLA (Hodgson et al., 2011; McDonald et al., 2003; Ordoñez et al., 2009), that increase plant flammability (Alam et al., 2020; Calitz et al., 2015; Grootemaat et al., 2015).

2 | MATERIALS AND METHODS

We evaluated the hypotheses relating to the direct and indirect effects of soil fertility on fire activity at regional scales across the five Mediterranean-type climate regions (MCRs) of the world based on global layers of spatially informed environmental data. We managed all those layers using the software QGIS 3.22 (QGIS.org, 2023) as described below.

2.1 | Bioclimatic zones

We first selected the MCRs worldwide based on the ecoregions map of Olson et al. (2001). Then, to define bioclimatically homogeneous zones, we intersected this map with the Köppen–Geiger climate classification map available from Beck et al. (2018), at ~10 km resolution (0.083°-pixel size). For this, the Köppen–Geiger layer was reclassified considering the first two criteria of this hierarchical classification system (i.e., climate group and seasonal precipitation type). Then, the raster layer was vectorized resulting in 1219 polygons (i.e., bioclimatic zones, hereafter). Cold and polar bioclimatic zones (respectively, D and E in the Köppen–Geiger climate classification system) were discarded, since they corresponded to small mountainous regions, mainly in the Andes of central Chile. For the remaining 992 bioclimatic zones, we identified the following climatic types (Figure 1a): arid (BW), semiarid (BS), temperate with dry summers (Cs) and temperate without dry season (Cf). Then, non-burnable land uses were discarded using a 2010 land cover map with a pixel size of ~300 m (ESA, 2017). All pixels classified as cropland, urban areas, water bodies, and permanent snow and ice were removed. Bioclimatic zones with a burnable area smaller than 200 km^2 (mainly small islands) were discarded due to the low reliability of georeferenced data (cf. Pausas & Ribeiro, 2013). Therefore, we considered a total of 200 bioclimatic zones (our geographical study units), covering ca. 61% of the MCRs.

2.2 | Environmental data

In water-limited ecosystems (*sensu* Stephenson, 1990), the productivity gradient is inversely related to the aridity gradient. In fact, aridity has been used in MCRs to study fire activity across productivity gradients (Pausas & Paula, 2012). In addition, the climatic conditions that trigger the occurrence of wildfires in MCRs change geographically with aridity: the higher the aridity, the greater the dryness needed to propagate fires (Pausas & Paula, 2012). We used the de Martonne Aridity Index (MAI) as the climate controller of the spatial pattern of fire activity in our study area. This index is calculated using the annual precipitation (P) and the annual mean temperature (T) as follows: $MAI = P/(T + 10)$; therefore, the higher the MAI, the lower the aridity (de Martonne, 1926). This index was calculated for each pixel using the annual precipitation and annual mean temperature from the CHELSA data set averaged for the period 2002–2018 at ~1 km resolution (0.0083°-pixel size; Karger et al., 2017). Then, we obtained the median of MAI across pixels for each bioclimatic zone. Finally, we calculated the absolute difference between the MAI of each bioclimatic zone and the maximum MAI obtained for the whole set of bioclimatic zones evaluated. Thus, the higher the value of this corrected index (aridity index, hereafter), the higher the aridity.

To describe the soil fertility of each bioclimatic zone, we considered the following variables from the Global Soil Dataset for Earth System Modelling (Shangguan et al., 2014), at ~1 km resolution (0.0083°-pixel size): pH in KCl (pH), organic carbon (Corg), total nitrogen (Ntot), cation exchange capacity (CEC) and exchangeable aluminium (Al). For each bioclimatic zone, we obtained the median values of these variables across pixels at 4.5 cm depth. The organic carbon to total nitrogen ratio (C:N), which indicates the recalcitrance of the organic matter (Janssen, 1996), was also calculated by dividing, for each pixel, the Corg by the Ntot, and then obtaining the median value for each of the 200 bioclimatic zones. We further included the phosphorous concentration in apatite (Papa) at 50 cm depth from the Global Gridded Soil Phosphorus Distribution Maps (from ORNL DAAC) (0.5°-pixel size; Yang et al., 2014). Apatite accounts for 95% of the total phosphorous in igneous rock, and its weathering releases inorganic phosphate available for plants and microorganisms; the older the soil, the lower the Papa (Lambers & Oliveira, 2019).

In MCRs, net primary productivity (NPP) is considered as an adequate proxy for fuel loading and continuity, where the higher the NPP, the higher the fire activity (Pausas & Paula, 2012; Pausas & Ribeiro, 2013). For each bioclimatic zone, we obtained the median value of NPP from the MODIS/Terra NPP data set (MOD17A3HGFv006; Running & Zhao, 2019) for the period of 2002–2018 at ~500 m resolution (0.0042°-pixel size). This data set derives annual NPP from the sum of all 8-day net photosynthesis products in a given year, which is calculated as the difference between the gross primary productivity and the maintenance respiration.

Finally, we obtained the fire activity for each bioclimatic zone based on the number of hotspots using the MODIS active fire location product (MCD14ML). We selected both Terra and Aqua satellites to minimize the number of bioclimatic zones with zero hotspots, and considered hotspots with a detection confidence of 70% or higher occurring from 2002 to 2022 (both included). The fire activity index for each bioclimatic zone was then defined as the logarithm of the number of MODIS hotspots in each bioclimatic zone divided by the size of the bioclimatic zone, rescaled from 0 to 1 (Pausas & Ribeiro, 2013; see resulting map in Figure 1b).

The frequency of ignitions plays a relevant role in the fire activity of a territory, as has been shown in several regions of the world for both anthropogenic (Gómez-González et al., 2019; Syphard et al., 2017) and natural ignitions (Abatzoglou et al., 2016; Pérez-Invernón et al., 2021). However, to our knowledge, there is not an a priori hypothesis of a possible relationship between soil fertility and the frequency of ignitions, whether natural or anthropogenic (see more details in Appendix S1). Therefore, ignition sources were not included in our model.

2.3 | Statistical analyses

All environmental data were available for 167 of the 200 bioclimatic zones, and thus, only those 167 bioclimatic zones were considered for the statistical analyses. The edaphic variables were summarized in two orthogonal dimensions of variation by a principal component analysis using the *prcomp* function of the *stats* library of the *R* software (R Core Team, 2022). Variables were log-transformed, centred and scaled prior the analyses. We then fitted

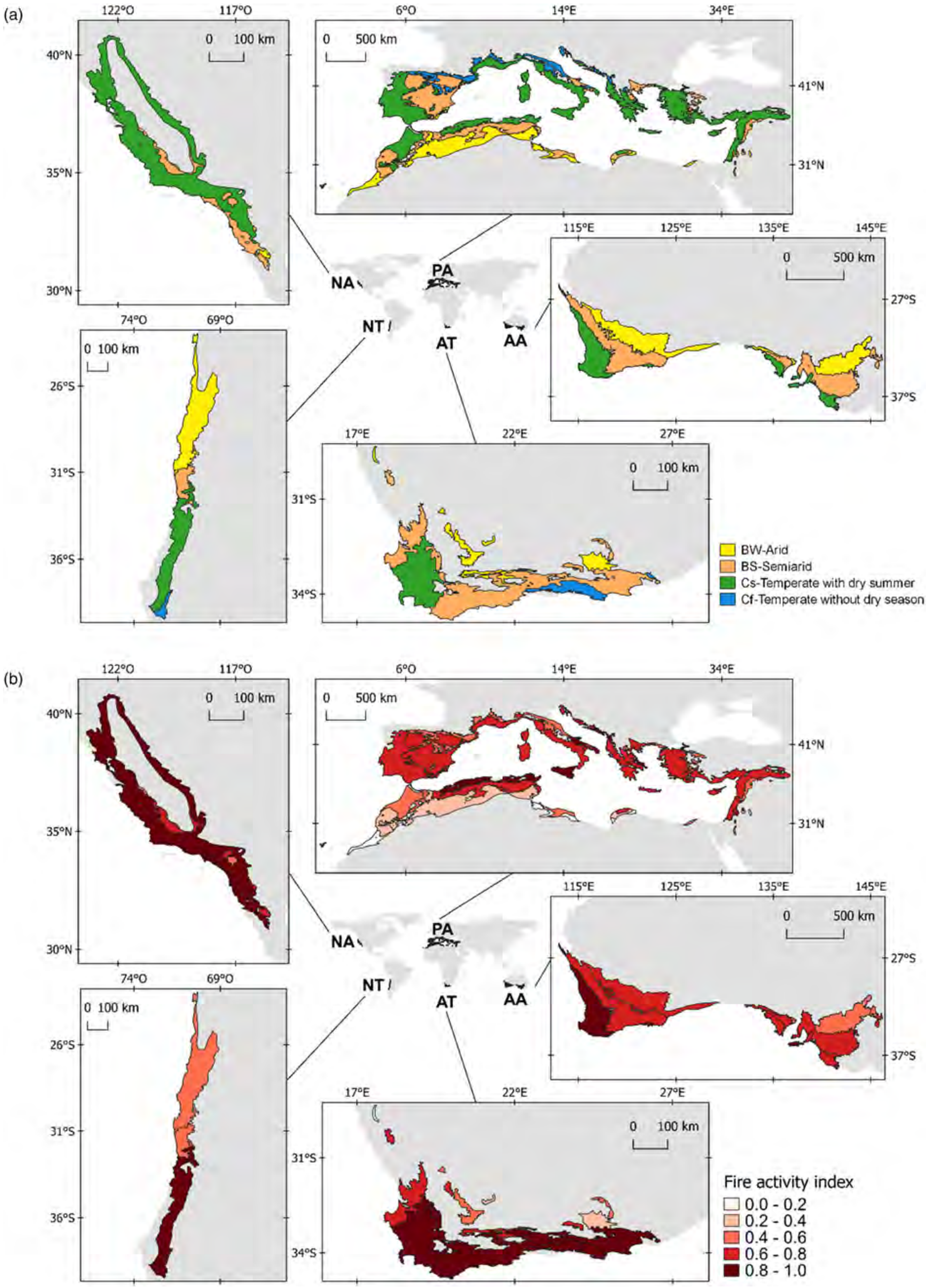

FIGURE 1 Global maps of the studied bioclimatic zones within the Mediterranean-type climate regions (MCRs). For the analyses, non-burnable areas were excluded (see detail in the Materials and Methods section). Bioclimatic zones were defined according to Olson et al. (2001) and the Köppen–Geiger climate classification (a). The fire activity *sensu* Pausas and Ribeiro (2013) in each bioclimatic zone is show in panel b. AA, Australasian (Southern Australia); AT, Afrotropical (Cape Region); NA, Neartic (California); NT, Neotropical (central Chile); PA, Paleartic (Mediterranean Basin).

a structural equation model (SEM; Kline, 2015) to evaluate the effects of climate and soil fertility on the fire activity through their impacts on the fuel, using the bioclimatic zone as sampling unit ($n = 167$).

Our initial hypothetical model proposed that the interaction between climate and soil fertility determines the amount, moisture and quality of the fuel in each bioclimate zone, and thus their propensity to burn (Figure 2). Climate was described by the aridity index, and soil fertility by the first two PCA components. We used NPP as a proxy of fuel loading, whereas fuel moisture and fuel quality were included in the model as latent variables. In the initial model, we proposed that both climate and soil fertility directly influence each of the fuel characteristics: amount, moisture and quality (see references in the Introduction). In addition, we included the effect of the climate on soil fertility, since climate affects both biological and geochemical processes determining the availability of nutrients in the soil: mineralization rates, mechanical rock weathering, nutrient leaching or erosion (Delgado-Baquerizo et al., 2013). Furthermore, we considered positive feedbacks between NPP and soil fertility, since plant biomass (using NPP as a proxy) provides many of the mineral nutrients in the soil, which in turn facilitate plant growth (Lambers & Oliveira, 2019).

The initial model was evaluated with the library *sem* of the *R* software (Fox et al., 2022) based on the correlation matrix to obtain the standardized coefficients relating each pair of variables (Grace, 2006; Kline, 2015). The analysis indicated that the initial model was over-parametrized, so it was simplified by eliminating latent variables and non-significant relationships. The model's fit was assessed based on the likelihood ratio χ^2 and the Steiger–Lind root mean square error of approximation (RMSEA; Kline, 2015). The spatial autocorrelation of the model was evaluated by means of Moran's I autocorrelation index of the residuals, using the spatial centroid for each bioclimatic zone. This last analysis was performed with the *ape* library in *R* (Paradis et al., 2004).

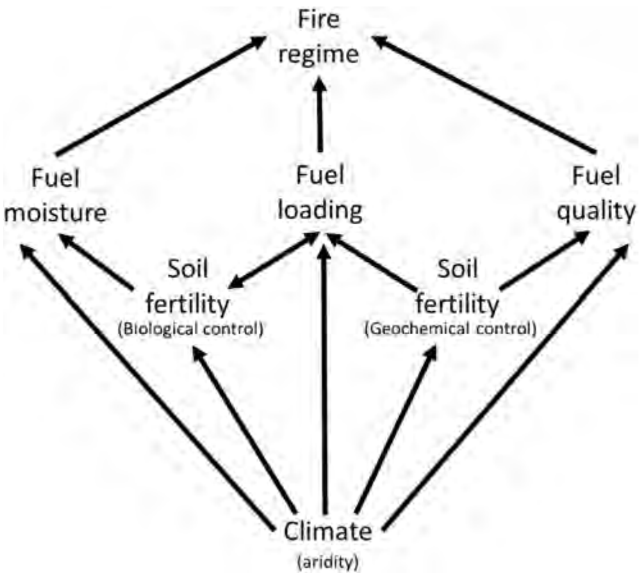

FIGURE 2 Initial hypothetical model of the effect of climate and soil fertility on fire activity in Mediterranean-type climate regions (MCRs) through fuel loading, fuel moisture, and fuel quality.

A brief description of the set of variables used in the SEM, as well as the original data sources is available in Table 1. In addition, a biplot matrix of the variables involved in the SEM is available in Figure S1.

3 | RESULTS

3.1 | Soil fertility dimensions

The first and second components of the PCA performed with soil properties describe the soil fertility of the bioclimatic zones (hereafter, soil-PC1 and soil-PC2; Figure 3; see Table S1 for full results). Soil-PC1 explained 39.5% of the total variance and was strongly and positively correlated with Corg, Ntot, C:N, and CEC, indicating that higher soil-PC1 values corresponded to more fertile soils due to the higher content of recalcitrant organic matter (Schroth & Sinclair, 2003). Soil-PC2 explained 24.0% of the variance and was strongly correlated with exchangeable Al (negatively) and pH (positively). Therefore, high soil-PC2 values corresponded to basic soils with low exchangeable Al, and thus, more fertile (Schroth & Sinclair, 2003). The geographical pattern of soil-PC1 and soil-PC2 is shown in Figure 4a,b, respectively.

3.2 | Structural equation modelling

The best-fitted model is shown in Figure 5. Both χ^2 and RMSEA did not significantly differ from 0, indicating that our model adequately described the data (Kline, 2015). The strongest relationship was found between the aridity index and soil-PC1 (negative). The aridity index was also significantly related to NPP (negatively) and soil-PC2 (positively), and more weakly to fire activity (positively). Both NPP and soil-PC2 were related to fire activity (positively and negatively, respectively). NPP and soil-PC1 covaried (positively), whereas soil-PC2 was negatively related to NPP.

By eliminating the latent variables, we include a correlational path between soil-PC1 and soil-PC2, which at a first glance might be counter-intuitive since these are principal components, which are (by definition) orthogonal. However, for this being true in our model, the net correlation should be zero. In a SEM, the correlation between two endogenous variables (in this case, soil-PC1 and soil-PC2) that are affected by the same primary variable (aridity index) is equal to the product of the two paths from the primary variable (Grace, 2006; Kline, 2015). Therefore, if our hypothetical model is true, then the correlation between soil-PC1 and soil-PC2 in the SEM should be equal, but with a different sign, to the product of the paths from the aridity index. In our case, the correlation path between soil-PC1 and soil-PC2 was 0.17, which is equal (but with a different sign) to the product of the coefficients from the aridity index to each of the soil-PCs ($-0.62 \times 0.28 = -0.17$). Such results confirm

TABLE 1 Description and data source of the variables used in this study.

Variable	Description	Data source
Aridity index	Absolute difference between the Martonne index of each bioclimatic zone and the maximum Martonne index obtained among all bioclimatic zones assessed, with higher values indicating greater aridity. The Martonne index was calculated by dividing the annual precipitation by the mean annual temperature plus 10.	CHELSA data set[a]
Soil fertility under biological control (soil-PC1)	Scores of the first axis of the principal component analysis summarizing the edaphic variables. It correlates positively with recalcitrant organic matter content.	Global Soil Dataset for Earth System Modelling[b] and Global Gridded Soil Phosphorus Distribution Maps[c]
Soil fertility under geochemical control (soil-PC2)	Scores of the second axis of the principal component analysis summarizing the edaphic variables. High values correspond to basic soils with low concentration of exchangeable aluminium.	Global Soil Dataset for Earth System Modelling[b] and Global Gridded Soil Phosphorus Distribution Maps[c]
Net primary productivity (NPP)	Annual difference between gross primary productivity and maintenance respiration obtained from the MODIS spectroradiometer of the Terra satellite.	MOD17A3HGF product v006[d]
Fire activity	Logarithm of the number of hotspots detected by the MODIS spectroradiometer of the Terra and Aqua satellites divided by the size of the burnable area and rescaled from 0 to 1.	MCD14ML product[e]

Note: References of the data sources are summarized in the table footer.

[a] Karger et al., 2017.

[b] Shangguan et al., 2014.

[c] Yang et al., 2014.

[d] Running & Zhao, 2019.

[e] 10.5067/FIRMS/MODIS/MCD14ML.

the statistical independency of the two principal axis of the PCA and rule out errors in the estimation of the paths from the aridity index to the soil variables (soil-PC1 and soil-PC2). Indeed, the alternative model that exclude the path between soil-PC1 and soil-PC2 did not fit the data, since χ^2 and RMSEA were significantly different from 0 ($\chi^2 = 8.85$, df = 3, $p = 0.031$; RMSEA 90% confidence interval: [0.03–0.20]; Figure S2).

The standardized direct and indirect effects of soil fertility (i.e., soil-PC1 and soil-PC2), aridity index and NPP on fire activity are summarized in Figure 6. Soil-PC1 did not directly or indirectly affect fire activity. The total effect (i.e., the sum of the direct and indirect effects) on fire activity was positive for NPP and negative for both soil-PC2 and aridity index. Net primary productivity was the variable that most strongly affected fire activity (standardized effect size: SES = 0.44), followed by the soil-PC2 (SES = −0.35) and the aridity index (SES = −0.18). The effect of NPP on the fire activity was direct, whereas the soil-PC2 and the aridity index affected the fire activity both directly (respectively, SES = −0.25 and SES = 0.18) and indirectly (respectively, SES = −0.11 and SES = −0.36). The residuals of the final SEM model were not spatially aggregated (Moran's $I = 0.035$, $p = 0.094$), suggesting that we are not inflating the Type-I error.

4 | DISCUSSION

As proposed, soil fertility significantly contributes to explain the geographical variability in fire activity across Mediterranean-type climate regions (MCRs) worldwide. Fires were more frequent in ecosystems with nutrient poor soils, particularly acidic soils rich in exchangeable aluminium (i.e., lower values of soil-PC2). The tight relationship we observed between pH and exchangeable aluminium can be explained by the increased solubility of aluminium as soil acidity increases (Schroth & Sinclair, 2003), a geochemical process shaped by bedrock and climate during pedogenesis (Lambers & Oliveira, 2019). Exchangeable aluminium is toxic to plants and edaphic microbiota, and reduces both root growth and soil nutrient availability (Lambers & Oliveira, 2019). Under such soil conditions, plants can be expected to grow slowly and to develop small, dense leaves with low nutrient concentrations and slow decomposition rates (Hodgson et al., 2011; McDonald et al., 2003; Ordoñez et al., 2009)—a suite of traits that increases flammability (e.g., Calitz et al., 2015; Grootemaat et al., 2015; Mason et al., 2016; see further details in the Introduction). Therefore, the higher fire frequency in acidic soils with high exchangeable aluminium concentration (i.e., low soil-PC2) can be explained by the higher flammability of plants growing under nutrient-limited soils. In the long term, this low fertility is maintained by a positive feedback, as frequent fires in these flammable vegetations reduce the local nutrient pools of the soil (Hinojosa et al., 2021; Pellegrini et al., 2018), favouring the development of more flammable plant communities that promote higher fire frequency (Wood & Bowman, 2012). Likely, this fire-soil feedback promoted the evolution of a well-adapted and biodiverse flora in nutrient-poor, fire-prone ecosystems (Cowling et al., 1996). The long-term relation between unfertile soils and fire is further

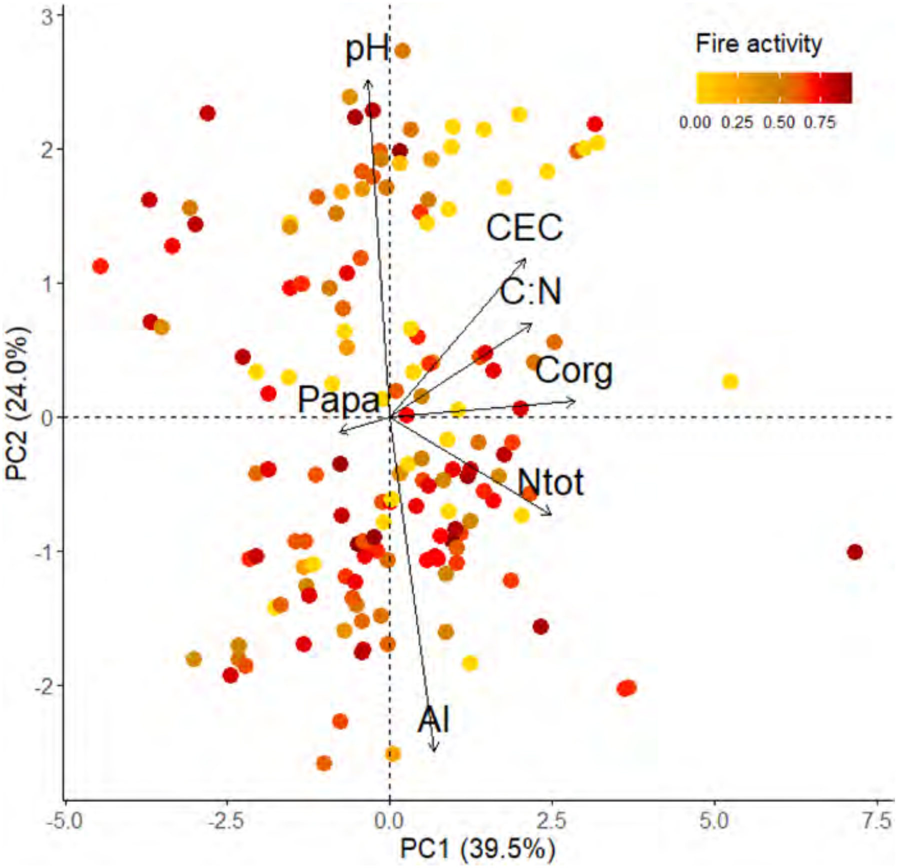

FIGURE 3 Principal components analysis (PCA) of soil characteristics across bioclimatic zones within the Mediterranean-type climate regions (MCRs) of the world. The symbols' colouration indicates the fire activity of the bioclimatic zones (from 0 to 1, unitless). Al, exchangeable aluminium; CEC, cation exchange capacity; Corg, organic carbon; C:N, organic carbon to total nitrogen ratio; Ntot, total nitrogen; Papa, phosphorus in apatite; pH, pH in KCl.

supported by the predominance of certain postfire regeneration traits among plants of regions with poor soils (Keeley et al., 2012) such as serotiny, a trait in which plants put up a significant amount of carbon into building cones or fruits to protect from fires and predators the valuable nutrients of their seeds (Keeley et al., 2011; Lamont et al., 2020).

Our results further emphasize the predominant role that fuel loading has on fire activity in MCRs. First, NPP was the major modulator of fire activity in our model. In fact, the effect of NPP on fire activity was 2.4 times greater than the direct effect of the climatic conditions. Moreover, aridity indirectly decreases fires by limiting plant growth (i.e., decreasing NPP) and thus the fuel loading. Therefore, our results support previous research at regional and global scales, indicating that fire activity in MCRs is limited by the amount and connectivity of fuels (Holz et al., 2012; Krawchuk & Moritz, 2011; Pausas & Paula, 2012; Pausas & Ribeiro, 2013). Nevertheless, aridity also affected fire activity directly as arid conditions dry up fuels and increase their flammability. Hence, the predicted drier conditions in MCRs under global warming will promote wildfires where the amount and connectivity of fuels allow fire to spread (i.e., in regions with drought-driven fire regimes; Pausas & Paula, 2012; Turco et al., 2018).

We found that the geographic variability in NPP across MCRs is under strong climate control, following global patterns (Cramer et al., 1999). In addition, NPP and the biological component of soil fertility (soil-PC1) covaried, indicating that soils with high organic matter provide nutrients that enhance plant productivity, which in turn provide further organic matter into the soil (Schroth & Sinclair, 2003). Finally, NPP was also negatively related to the soil fertility dimension under geochemical control (soil-PC2), indicating that NPP is lower on basic soils. Globally, basic soils typically develop under arid conditions that favour the accumulation of calcium as carbonates (Slessarev et al., 2016), and our positive relationship between aridity and soil-PC2 supports this pattern for MCRs. Hence, the relationship between NPP and soil-PC2 revealed by our analysis might reflect an indirect effect of aridity on productivity through the soil properties (Figure 6). Nevertheless, the edaphic variables associated with soil-PC2 (pH and aluminium concentration) are strongly dependent on the bedrock and the age of the soil (Lambers & Oliveira, 2019). The Mediterranean-type climate regions, despite sharing similar climatic conditions, develop under different bedrocks and have differing soil ages: from the oligotrophic soils derived from ancient sandstones in the MCRs of southwestern South Africa and southwestern Australia, to the

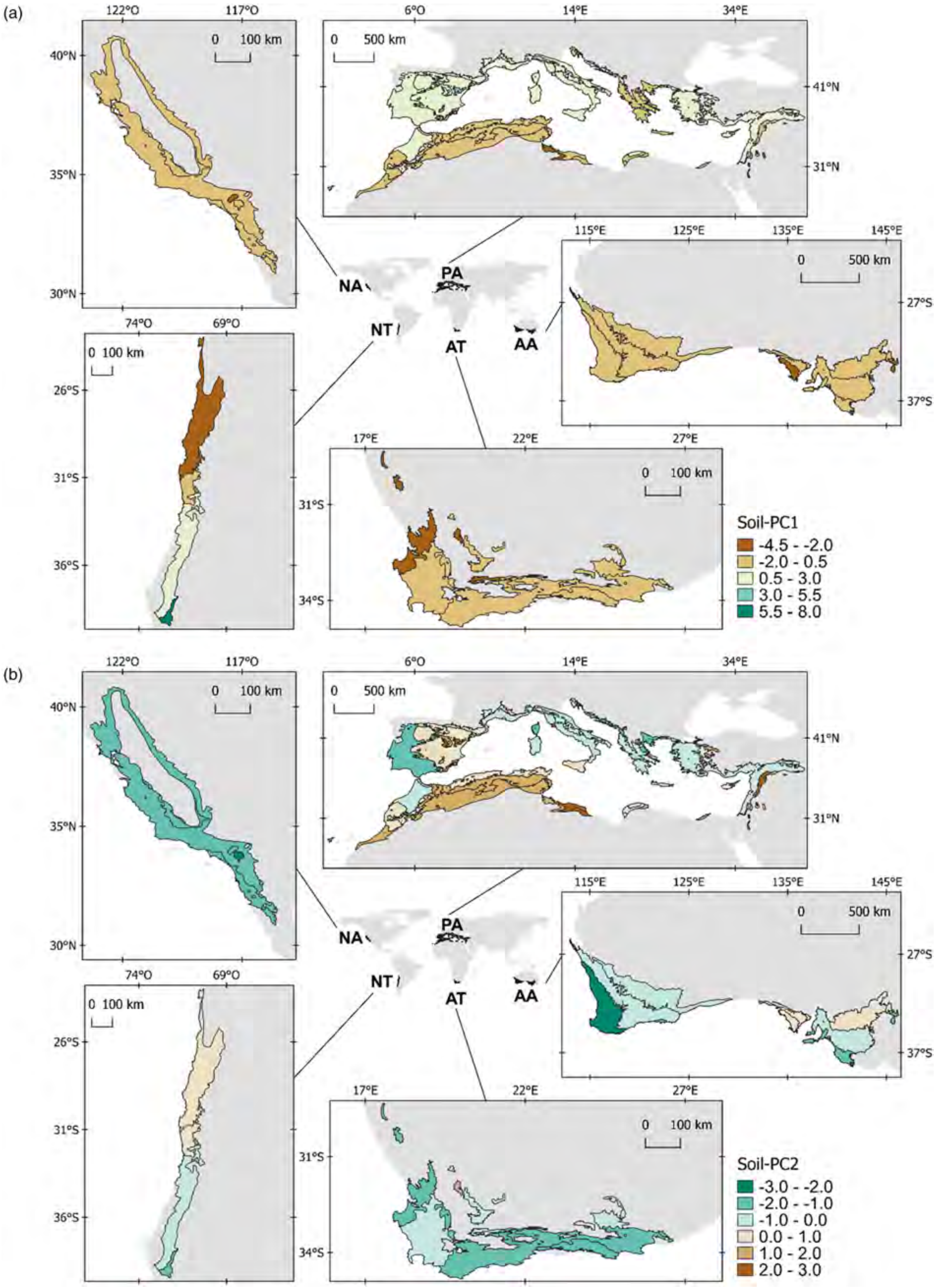

FIGURE 4 Global maps of the biological (soil-PC1; a) and geochemical (soil-PC2; b) components of the soil fertility estimated through the PCA for the studied bioclimatic zones (Figure 3 and Table 1). For the analyses, non-burnable areas were excluded (see detail in the Materials and Methods section). AA, Australasian (Southern Australia); AT, Afrotropical (Cape Region); NA, Neartic (California); NT, Neotropical (central Chile); PA, Paleartic (Mediterranean Basin).

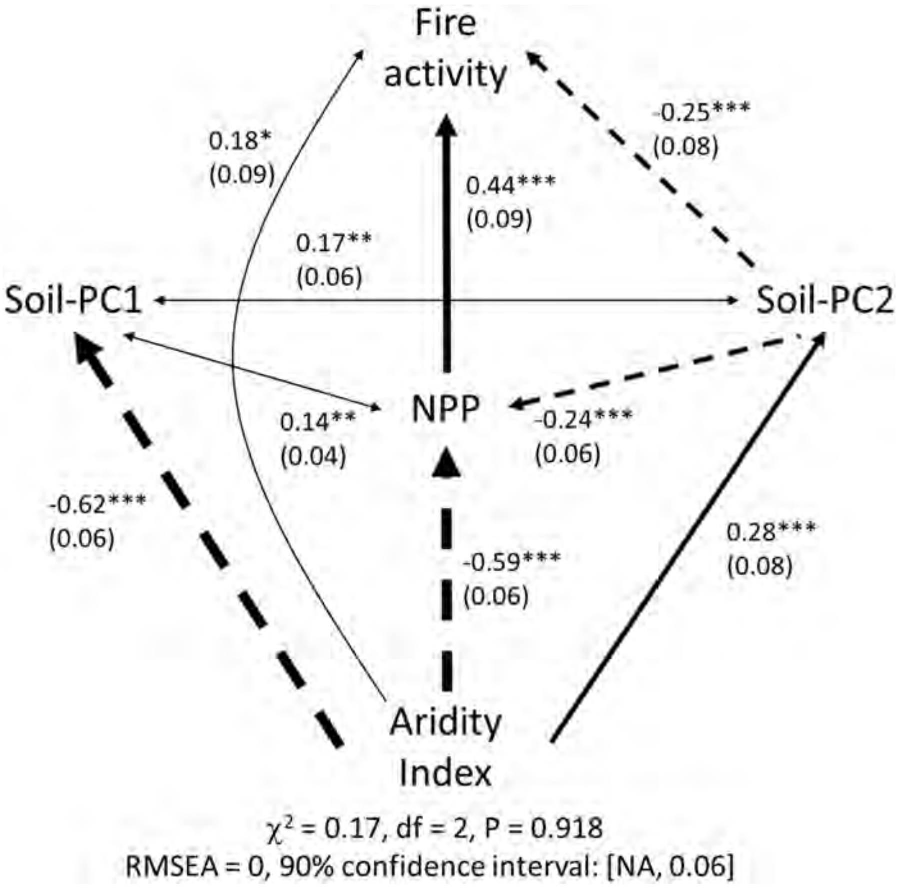

FIGURE 5 Summary of the structural equation model fitted to evaluate the effect of aridity and soil fertility (soil-PC1 and soil-PC2) on the fire activity across bioclimatic zones within the Mediterranean-type climate regions (MCRs) of the world. Fuel loading was estimated by the net primary productivity (NPP) of each bioclimatic zone. See Table 1 for a brief description of the variables. Continuous and discontinuous lines indicate positive and negative relationships, respectively. Line width is proportional to the strength of the relationship. Standardized coefficients of the relationship are show next to the corresponding arrow (with standard errors in brackets). The significance of the relationship is indicated with asterisks: ***$p<0.001$, **$p<0.01$, and *$p<0.05$. Overall fit statistics for the model are show below the path diagram. RMSEA, Steiger–Lind root mean square error of approximation.

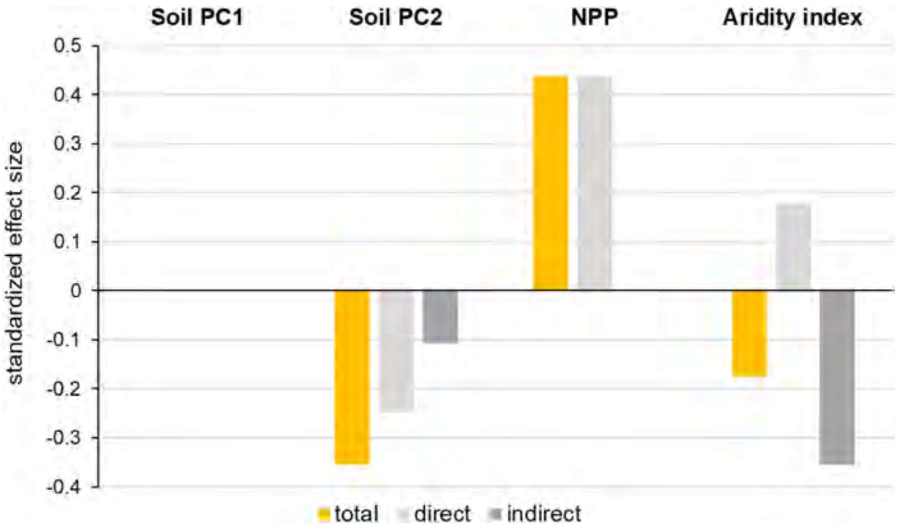

FIGURE 6 Standardized effect size (SES) of the soil fertility (soil-PC1 and soil-PC2, see Figure 3 for details), the net primary productivity (NPP), and the aridity index on the fire activity of the bioclimatic zones within the Mediterranean-type climate regions (MCRs) of the world.

soils derived from recent volcanic deposits in the MCRs of central Chile (Keeley et al., 2012). Such geological differences among continents could contribute to explain the role of soil on fire proneness across bioclimatic zones in MCRs. When assessing the geographical pattern of the residuals from the SEM fit, we did not find a spatial autocorrelation, suggesting that the model performs well in explaining the geographical variability.

In summary, there is a complex interaction between climate and soils that modulates fire activity (Figure 5). The role of soil fertility is likely explained by its effect on intrinsic properties driving the flammability of fuels, which further leads to an increased fire activity and nutrient release from the system. Likely, this feedback maintains frequent fires in unfertile MCRs, promoting the evolution of a diverse and fire-adapted flora. We propose that, beyond fuel quantity and fuel moisture (both strongly affected by climate), fire occurrence also depends on the degree of flammability of fuels, which changes along the MCRs mainly as a function of the soil and, to a lesser extent, of the climate. Future experimental studies may further elucidate the specific mechanisms by which soil fertility affects the flammability of vegetation and the implications for the interacting species in the community. Moreover, the effect of soil fertility on fire proneness should be considered when modelling fire regimes in an increasingly flammable future.

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CONFLICT OF INTEREST STATEMENT

None of the co-authors has a conflict of interest to declare.

DATA AVAILABILITY STATEMENT

All data were obtained from published sources as indicated in the Methods section. The maps and the aggregated data are openly available in DRYAD at 10.5061/dryad.573n5tbdh.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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