Functional and compositional diversity display a maximum at intermediate levels of fire frequency when modeling the plant-fire feedback

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Abstract

Fires are generally considered to promote biodiversity, although this relationship can be affected by several factors, including fire regime and ecosystem type. Given the ongoing global change, a better understanding of this connection is needed to assess the extent to which projected increases in fire frequency may affect current biodiversity trends. A major challenge lies in vegetation-fire feedback, which often mediates the changes in fire regime. To shed light on the role of fires in promoting or limiting biodiversity, we studied the compositional and functional diversity of simulated plant communities as a function of different fire frequencies. We extended an existing model to include a large number of species. The model reproduces successional dynamics and is parameterized to represent Boreal and Mediterranean plant communities. Fire events are stochastic, with frequency that depends on the community flammability, and plants have different fire responses, thus representing a vegetation-fire feedback. For both ecosystems, we found that fires generally have a positive effect on diversity. All of the biodiversity indicators analyzed, to some extent, peaked at intermediate fire frequency. Interestingly, we observe a decoupling between compositional and functional diversity. These results are related to the vegetation-fire feedback and underline its importance for biodiversity in fire-prone ecosystems.

Introduction

Fires play a key role in the Earth system, as they occur in most ecosystems that support sufficient biomass to burn (Archibald et al., 2013). Over millennia, fires have been crucial in shaping the composition and distribution of biomes (Bond and Keeley, 2005) since they first appeared, concomitant with the origin of terrestrial plants (Pausas and Keeley, 2009). Fire occurrence is strongly controlled by climate, and requires specific weather conditions (Boer et al., 2017). At the same time, wildfires are also dependent on vegetation, which constitutes the main fuel for fires (Bowman et al., 2020). In fire-prone ecosystems, vegetation influences the local fire behavior through its flammability, which arises from key functional traits of plants relating to, e.g., the quantity, quality, moisture content, and aeration of plant biomass (e.g. Pausas and Keeley, 2021; Simpson et al., 2022). This creates a fire-vegetation feedback, in which plant community composition responds to and influences the frequency, intensity, and extent of fire events, that is the fire regime (Archibald et al., 2013). The prevailing fire regime is then the result of climatic and meteorological drivers, mediated by these fire-vegetation feedbacks (Archibald et al., 2018).

Plants have also adapted to survive and thrive in fire-prone ecosystems, evolving strategies that can lead to persistence at different levels: combustion-stimulated germination or post-fire seed release in crown systems (i.e., serotiny) grant population persistence; plant individual persistence is granted instead by the ability to resprout after fires, i.e., a set of plant strategies connected to protecting vital tissues above and below-ground (Clarke et al., 2013). Together, these strategies are the so-called fire responses (Pausas, 2019). The combination of plant traits related to flammability and to post-fire responses can lead to the emergence of a positive vegetation-fire feedback, playing a key role in some ecosystems around the world. A positive feedback can emerge in the presence of fire-prone vegetation that stimulates fires and also has strong post-fire recovery: more fires enhance plant growth, in turn leading to a larger number of fires. This is the case, for example, in tropical grasslands and savannas, dominated by flammable and fire-stimulated C_4-grasses (Bond, 2008). The same positive feedback can also sustain ecosystems

where fires rarely occur, such as some tropical forests, where vegetation limits fire spread by creating a humid environment and reducing wind speeds, while at the same time not having any specific response to fire (e.g. Charles-Dominique et al., 2017).

Fire has been identified as a critical driver of biodiversity and ecosystem functioning in fire-prone ecosystems (Bond and Parr, 2010; He et al., 2019; Kelly et al., 2020; Pausas and Keeley, 2019). Generally, fires are thought to promote turnover and diversification of plant populations, and can promote the coexistence of plant species (Brooks et al., 2004; He et al., 2019; Pausas and Ribeiro, 2017, and references therein): They reduce the dominance of the most competitive plant species and allow different species to dominate at different stages of post-fire succession. However, extreme conditions, e.g. very frequent or very infrequent fires, may reduce the overall biodiversity. Specifically, very frequent fires seemingly tend to exclude all plant species that have no response to fires, but also, for example, those with seedbanks that require longer periods to reach maturity, leading to population declines and even local extinctions (e.g. Bowman et al., 2013; Enright et al., 2015). Conversely, when fires are absent for decades or centuries, many shade-intolerant or fire-dependent species (e.g. conifers with serotinous cones) will have been excluded by stronger competitors for light and other limiting resources, or disappeared due to a lack of viable offsprings. Given these premises, functional and specific diversity is expected to peak somewhere in the middle between these two extreme scenarios, where fire-adapted and unadapted plant species can coexist. This is similar to what is postulated by the *Intermediate Disturbance Hypothesis* (IDH) (Connell, 1978; Huston, 1979), even though the IDH does not consider the fact that fire is an endogenous element in plant ecosystems (Bond and Keeley, 2005; Kelly et al., 2020). A hump-shaped relationship between plant diversity and fire frequency has been well supported (Dee and Menges, 2014; Gordijn et al., 2018; Pellegrini et al., 2023). In some studies, however, species richness and functional diversity monotonically decrease with increasing fire frequency, especially among woody species (He et al., 2019, and references therein). In fact, it has been argued that such discrepancies might be due to the difficulties in sampling a sufficiently large set of fire frequencies, or in sampling systems with species turnover along

the fire frequency gradient, rather than capturing responses of a fixed species pool (He et al., 2019). In a set of model experiments where fires were imposed as exogenous disturbances, a multimodal diversity-disturbance relationship emerged (Liao et al., 2022). Understanding the connection between wildfires and biodiversity in different fire-prone systems around the world is an important challenge given the ongoing biodiversity crisis and the new era of fire regime, with increasingly intense and extensive fires on the one hand, and increased fire suppression on the other (Cunningham et al., 2024; Kelly et al., 2020).

Here we set out to study the relationships between plant diversity and fire frequency, including compositional and functional diversity. We extend an existing theoretical model of plant and fire dynamics (Magnani et al., 2023), to include a large number of species. The model represents plant succession (following Tilman, 1994), species-specific fire responses, and fires as stochastic events whose occurrence depends on the flammability of plant communities. Thus, the model captures the existence of feedback between plant communities and fire frequency. We parameterize the model for real communities in the Mediterranean and Boreal ecosystems. Our analysis consists of three steps, answering the following research questions: i) How do fires impact compositional and functional diversity in Mediterranean and Boreal ecosystems, as compared to systems without fires? ii) How do both types of diversity depend on the fire frequencies that emerge within the fire ecosystems? iii) To what extent is a higher number of coexisting plant species associated with a larger range of competitive and fire response strategies? Our results show that fires promote biodiversity, as expected; furthermore, diversity indicators peak at intermediate fire frequency. The two types of diversity are not always strongly correlated within communities.

Methods

Competition model with stochastic fires

In order to explore fire-driven biodiversity in a general framework, we developed a conceptual model describing the dynamics of fire-prone plant communities, based on and extended from the work in Magnani et al. (2023). The model includes competitive plant dynamics during fire-free periods, stochastic fires, and post-fire recovery, and was used to study the relationship between plant characteristics, fire regimes, and alternative ecological states. We extended the original approach of (Magnani et al., 2023) , which represented three species, to represent a large number (N) of plant species.

The model represents the competition-colonization dynamics of plant species, following the classical approach of Tilman (1994). This is a proximal representation of plant competition for a single resource (mostly light in this and previous works (Baudena et al., 2020; Magnani et al., 2023)). Each species has a fixed position in the competition hierarchy, from the strongest ($i = 1$) to the weakest ($i = N$). The governing equation of the model for the plant cover $b_i(t)$ of species i is (analogously to Tilman, 1994):

$$\frac{db_i}{dt} = C_i b_i \left(1 - \sum_{j=1}^{i} b_j\right) - M_i b_i - b_i \sum_{j=1}^{i-1} C_j b_j \tag{1}$$

In this representation, each plant species can colonize both the empty space and the space occupied by inferior competitors. C_i is the maximum per capita colonization rate, which is multiplied by the population size b_i to obtain the fraction of space that species i would colonize per time unit in the absence of other species. This rate is then reduced by the crowding factor $\left(1 - \sum_{j=1}^{i} b_j\right)$, which quantifies the spatial restrictions to colonization due to the presence of superior competitors or of species i itself. M_i is the mortality rate, whereas the last term on the right-hand side of eq. 1 represents the superior species' skill to invade and colonize species i space, and can therefore be defined as a displacement term. In the absence of hierarchically

superior species, persistence of a species requires satisfying a simple condition, $C_i - M_i > 0$. This condition of existence is necessary for each species, albeit for species lower in the hierarchy ($i > 1$) it is not sufficient to ensure survival, due to the displacement term.

The fire-vegetation feedback and stochastic fire events are modeled as instantaneous, stochastic events, with a probability of occurrence that is exponentially distributed. The average fire return time (i.e., the mean time interval between two consecutive fire events) is inversely proportional to the flammable plants vegetation cover (Baudena et al., 2020; Magnani et al., 2023):

$$T_f = \frac{1}{\sum_{i=1}^{N} L_i b_i + \epsilon}$$

where L_i is the flammability of the species i, and the term $\epsilon = 10^{-3} yr^{-1}$ ensures the convergence of fire return time when the total plant cover is null. The stochasticity of the fire signal is simulated using a nonstationary Poisson process (Sigman, 2007) with rate $\lambda = 1/T_f$. The interarrival time of fires thus follows an exponential distribution, with a mean interarrival time depending on the vegetation cover and community composition in the preceding time-step. Furthermore, we imposed a realistic minimum fire return time of 2 years (following Baudena et al., 2020; Magnani et al., 2023).

Plant response to fire is represented by the parameter $0 \leq R_i \leq 1$. When a fire occurs, the cover of each species is reduced to a specific fraction determined by its fire response,

$$b_i(T_f) = R_i b_i.$$

We follow here the formulation introduced by Magnani et al. (2023), where the fire response R_i is a parameter that represents the different plant fire strategies at individual and population level. In this approach, following Pausas and Lavorel (2003), the different fire responses are ranked from no response for very low R_i values, to intermediate responses at population level (e.g. re-seeding), to high values at individual level (e.g. resprouting).

We investigated the relationship between diversity and fire return time in two iconic fire-prone systems: Mediterranean forests and shrublands, and Boreal forests. In Mediterranean-type

regions, the prevailing vegetation is composed of evergreen sclerophyllous-leaved shrublands, semi-deciduous scrub, and woodlands, whose high flammability leads to frequent, high-intensity summer fires (Keeley, 2012). These regions are often densely inhabited, and fire ignition is usually attributable to anthropogenic causes (Ganteaume et al., 2013). Boreal ecosystems are typically dominated by conifers with a ground layer vegetation of shrubs, low herbs, and moss. Aside from anthropogenic activity, fire ignition is often due to lightning, and fire hazard is spread over all seasons (Rowe and Scotter, 1973).

In an effort to represent realistic plant communities, we extrapolated the parameters related to succession (C_i and M_i in eq. 1) from scientific literature. To do so, we performed linear regressions for the colonization and mortality rates on the one side and the position in the hierarchy on the other, as parameterized and calibrated in Baudena et al. (2020) and Magnani et al. (2023) (see table A1-A2). Once these linear relationships were established, we generated the parameters C_i and M_i of our N species stochastically from these distributions:

$$C_i = \alpha_C i + \beta_C + \gamma_{C_i}$$

$$M_i = \alpha_M i + \beta_M + \gamma_{M_i},$$

where αs and βs are, respectively, the slopes and the intercepts of the regressions fig. A1, and γs are zero-mean gaussian noise terms, whose standard deviations are also determined from the standard deviation of the data around the linear regression (see table A3 and the vertical bars in fig. A1). As a further requirement, each generated species must satisfy the condition $C_i > M_i > 0$, i.e., it must be able to potentially persist in isolation. Moreover, as in the present paper we set a different number of species N, we rescaled the hierarchy so that the first and N-th species represent the boundaries of the parameter range provided by the regression models depicted in fig. A1. From the linear fits, the colonization rates are inversely related to the position in the hierarchy. This is reasonable since generally plants with better access to light are also slower in growing and colonizing than the less competitive ones — that is, trees generally grow slower

than shrubs and grasses. Interestingly, in the two ecosystems the regression of mortality rate as a function of hierarchy presents opposite trends, thus ensuring more generality to communities generation and, consequently, to the model results.

Finally, to explore a comprehensive variety of fire strategies, leading to a wide assortment of fire return times, we did not impose fixed values on the ecosystem's fire-responses and flammabilities — which lead to the fire-vegetation feedback. Thus, a variety of fire trait combinations is simulated: fire response R_i is sampled from a uniform distribution between 0.001 and 1, while flammability is defined as $L_i = 10^{-\theta}\, y^{-1}$, where θ is a random number uniformly distributed between $log_{10}(2)$ and $log_{10}(500)$ — thus, $0.002 \leq L_i \leq 0.5\ \mathrm{yr}^{-1}$, potentially representing an average fire return time varying between 2 and 500 years.

Simulations

We generated and simulated 1000 communities for each of the following cases: Mediterranean communities with i) $N = 10$ initial species (hereafter Med-10) and ii) with $N = 50$ initial species (hereafter Med-50); and iii) Boreal type communities with $N = 10$ initial species (hereafter Bor-10). The limited number of initial species in the Boreal communities reflects the smaller species pool and lower biodiversity of the Boreal ecosystems compared to those of the Mediterranean. In fact, among these three types of communities, Med-50 and Bor-10 can be considered the most realistic, with Med-10 providing a reference to study the separate effects of initial species richness (through comparison with Med-50) and the effect of ecosystem type (through comparison with Bor-10).

Initial conditions

Every community, initially composed of N species randomly generated as explained in section "Plant communities in the Mediterranean and Boreal forests", underwent $N + 2$ runs, each with different initial conditions, determined as follows:

- 1 initial condition corresponding to small and equal vegetation cover for all species:

$$b_i(0) = 0.01, \ \forall i = 1, 2, ..., N$$

- 1 initial condition corresponding to equal vegetation cover for all species, with larger values than in the previous case, given by:

$$b_i(0) = \frac{1}{N+1}, \ \forall i = 1, 2, ..., N$$

- N initial conditions with high vegetation cover for a single species and low for all the others, leaving an initial portion of empty space equal to 0.1:

$$b_i(0) = 0.01, \ \forall i = 1, ..., j-1, j+1, ..., N$$

$$b_j(0) = 0.91 - 0.01N$$

Such initial conditions are designed to meet the requirement of total vegetation cover not exceeding the unity (Tilman, 1994).

Numerical integrations

The model has been coded in Fortran; some results were also reproduced with Python code (see section "Data and Code Availability'). All the numerical integrations presented below are performed using a Runge-Kutta 4 method, with runs of $10^4\,y$ and time steps of $1\,day$.

The different set of initial conditions brings the total number of simulations to 12,000 for Med-10 and Bor-10 and to 52,000 for Med-50. Such large number of runs, together with their duration, allows for a proper statistical representation of these stochastic systems (Baudena et al., 2020; Magnani et al., 2023).

Analyses

We analyzed the time series obtained in the second half of each run, i.e., 5,000 years, considering the first half as spin-up time needed to reach a statistically steady state. Over the latter interval, we averaged each species' cover, acquiring a set of average cover values $\langle b_i \rangle$, which defined the state achieved by a community starting with a specific set of initial conditions. Furthermore, for every run we averaged the system's fire return time, obtaining a value $\langle T_f \rangle$ corresponding to each set of $\langle b_i \rangle$s. As shown in Magnani et al. (2023), running this model (with $N = 3$) multiple times can result in different final communities even when using species with the same set of parameters, due to different initial conditions and/or to the stochastic signal underlying fire occurrence. Thus, we expect multiple stable states are likely to exist also in the model with $N > 3$, and we chose a set of initial conditions and a large enough number of simulations to capture such alternative ecosystem states, as they possibly enlarge and enrich the diversity of the final communities represented. Yet, we deem that a thorough identification of all possible ecosystem states is not necessary to reach the aims of this paper.

In the following, we introduce how we estimated quantitatively the biodiversity of the simulated ecosystems, using four indicators that account for both compositional and functional diversity, and how we answered the three research questions by analyzing their relationships with fire return time.

Compositional diversity indicators

We estimated ecosystems' biodiversity using a set of biodiversity indicators based on the *composition* of the plant communities (Noss, 1990), namely Species Richness and the Inverse Simpson Index. They are defined and estimated as follows:

- *Species Richness S* is the number of coexisting species in the community (considering as minimal threshold for the presence of each species an average vegetation cover $\langle b \rangle \geq 10^{-3}$).
- *Inverse Simpson Index I*, which evaluates the concentration of different surviving species

within the community (Simpson, 1949), is defined as:

$$I = \frac{1}{\sum_{i=1}^{N} p_i^2},$$

where p_i is the relative abundance of species i, calculated from cover:

$$p_i = \frac{b_i}{\sum_{j=1}^{N} b_j}.$$

Note that, in each summation, only S species survive among the N initial species. Therefore, $N - S$ b_j terms are null.

Functional diversity indicators

Another important biodiversity attribute is the *function*, which involves ecological and evolutionary processes, including gene flow, disturbances, and resource utilization and cycling (Noss, 1990). We implemented functional diversity indices as represented in our model by the diversity of the plant species parameters in the final community assembly. To do so, we used the concept of *hypervolumes*, that is the volume in the trait (or parameter, in our case) space of the surviving species (Blonder et al., 2014; Mammola and Cardoso, 2020), and estimated for each community assembly its Functional Richness and Divergence as follows.

We considered the parameter space composed of the competition index i, the colonization rate C, the mortality rate M, the fire response R , and the flammability L. For the hypervolume estimation, the composition of each community was transformed into an input dataset, weighted using the species cover: each plant parameter set was repeated in the dataset $\langle b \rangle \cdot 10^3$ times, consistently with the threshold set to consider species presence in the resulting community. This had the effect of weighting the parameters according to the species cover.

To ensure each axis had comparable units (Blonder et al., 2014), the parameters were rescaled using a range normalization: being t the original value of a parameter, t_{min} and t_{max} the maximum and minimum value of that parameter, the parameter was normalized as $t' = (t - t_{min})/(t_{max} -$

t_{min}). The parameter range values were set as equal for all communities simulated in the two ecosystem types, to ensure comparability across them, with the only exception of i, whose range was kept consistently [1,10] for Med-10 and Bor-10 and [1,50] for Med-50.

The hypervolume of each community was then computed as a rescaled sample inferred from a Gaussian (`KernelDensity` function of the `sklearn.neighbors` Python library) of the input community datasets. The representation of an estimated hypervolume is reported in fig. B1 as an example. The calculation method implemented for the hypervolume estimation is a simplification of the original proposed by Blonder et al. (2014), which was developed to model high-dimensional and irregular populations (e.g., with holey distributions), while our modeled communities represent a relatively low-dimensional trait space ($5D$) and consist of sets of 50 unique points at most.

We then estimated the functional richness and divergence metrics from the constructed hypervolumes:

- *Functional Richness* F_R, which is the total amount of trait space available, was computed as the volume of the Convex Hull derived from the input hypervolume, using the `spatial.ConvexHull.volume` function of the `scipy` Python library (Virtanen et al., 2020).

- *Functional Divergence* F_D, which measures the density of the trait space, was computed as the average distance between the trait space centroid and random points within the boundaries of the hypervolume, using the `staila.distance.cdist` function from the `scipy` Pyhton library (Virtanen et al., 2020) to estimate the $5D$ distance.

The functional richness and divergence metrics were constructed based on those proposed by Cardoso et al. (2015) in BAT - Biodiversity Assessment Tools (`kernel.alpha` and `kernel.dispersion` functions, respectively). See section "Data and Code Availability' for the full implementation of the code.

Fire-biodiversity analyses

To answer the first research question and investigate the role of fires for community diversity, we analyzed the difference in diversity indicators between communities simulated with and without fires. Specifically, we calculated the differences in diversity indicators of the simulated resulting communities obtained by running the model for the same initial sets of species with fires turned on and off — the latter case being the standard Tilman model. Taking the Species Richness difference as an example, we estimated $\Delta S = S_{\text{fire}} - S_{\text{no-fire}}$, with S_{fire} being the Species Richness of a community resulting from our model simulation, and $S_{\text{no-fire}}$ the Species Richness of the community resulting from the model without fires — which we simply calculated analytically as the Tilman equation equilibrium for the same initial set of species. The distributions of these biodiversity-indicator differences were tested to assess whether the difference between indicators built on paired ecosystems — i.e., the final communities achieved after running the model with and without fires — was significantly different from zero. Inverse Simpson Index, Functional Richness, and Functional Divergence difference distributions were tested through the Wilcoxon signed-rank test. Since the rank test cannot be applied to discrete distributions, Species Richness difference distributions were tested via the Sign Test. The tests were conducted using respectively the `scipy.stats.wilcoxon` function of Python library SciPy (Virtanen et al., 2020) and the `statsmodels.stats.descriptivestats.sign_test` function of Python library StatsModels (Seabold and Perktold, 2010).

To answer the second question, we analyzed the biodiversity indicators of the resulting communities as a function of their fire return times. We performed quantile regressions to test the significance of the relationship, since the biodiversity indicators are bounded to minimum values (1 for S and I, 0 for F_R and F_I), and the homogeneity of their variance across the fire return time gradient could not be assumed (Belyea, 2007). We used the 95th, 85th and 75th quantiles to focus on the trends of the diversity maxima and to estimate the functional relationship near the upper limits of the data distribution (Belyea, 2007, and references therein). For each quantile,

we fitted the data with first- to fifth-order polynomial quantile regressions and selected the most performing polynomial regressions based on the Akaike Information Criterion and the Walt Test of significance (Koenker and Portnoy, 1996).

For the third question, we estimated the correlations between compositional and functional diversity indicators, to investigate whether the different indices estimated from the same simulated communities resulted in similar patterns. To test the correlation, we used the Pearson correlation coefficient r_{xy}, computed with the `scipy.stats.pearsonr` function (Virtanen et al., 2020).

Results

The distributions of the differences between the biodiversity indicators estimated for communities with and without fires (fig. 1) showed that, on average, fires promote biodiversity, regardless of ecosystem type. From the Wilcoxon signed-rank test (whose statistics and p-values are reported in table C2 in Appendix C), the distributions underlying the biodiversity indicator differences resulted centered around a value significantly greater than 0 (fig. 1), with the exception of the distribution of the Functional Richness differences ΔF_R for the Med-10 and Med-50 ecosystem types (panel C in fig. 1). Furthermore, the distributions of ΔI and ΔF_R resulted skewed towards positive values, meaning that there were more communities with increased levels of biodiversity due to the presence of fire than with reduced levels. Likewise, the median of the distribution of the Species Richness differences ΔS, which excludes null values, resulted significantly greater than zero from the Sign test (whose statistics and p-values are reported in table C1 in Appendix C). However, the test findings might appear in contrast to what a visual inspection of the Med-10 and Med-50 distributions shows, i.e., distributions evenly centered around zero. This discrepancy is likely due to the numerous null values in the subsets, which influence the distributions but are excluded from the test, a characteristic that inherently limits the robustness of the result.

To answer the second research question, plotting the indicators of compositional and func-

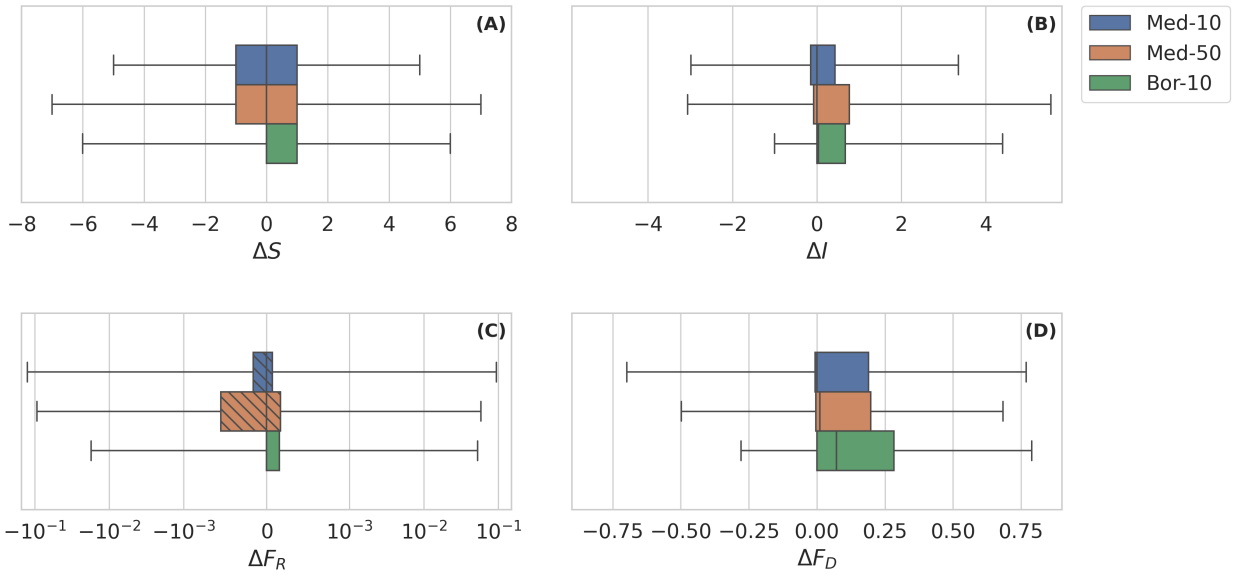

Figure 1: Distributions of the difference between biodiversity indicators for communities with fires (simulated with the fire-vegetation model) and without fires (calculated as equilibria of the Tilman model): A) Species richness (ΔS); B) Inverse Simpson Index (ΔI); C) Functional Richness (ΔF_R) and D) Functional Divergence (ΔF_D). The colors identify the distributions for the ecosystem types and initial species number (see legend). Distributions that resulted centered around a value lower than or equal to 0 from the Sign or the Wilcoxon signed-rank test are marked with hatched signs.

tional diversity as a function of the average fire return time, we observed that, although the communities show a wide spread of diversity values, the maximum level of biodiversity occurred at intermediate fire frequency (Figure2 and 3). Both compositional diversity indices S and I reached their maximum value at intermediate return times, and local minimums at the two extremes of the fire axis (fig. 2). We observed this pattern in all three types of simulated communities. Although the polynomial order of the best-fit curves was not identical between quantiles and community types, all curves reflected a hump-shaped pattern. Incidentally, we notice that the highest level of Species Richness S (fig. 2, top panels) was observed among Med-50 communities (9 coexisting species), followed by the Bor-10 communities (maximum of 8 coexisting

species), and the Med-10 communities (max. 6 coexisting species). Similarly, the Inverse Simpson Index I values (fig. 2, bottom panels) were highest for the Med-50 communities (6.8), followed by the Bor-10 communities (5.4) and the Med-10 communities (4.35). These differences were due to the different size of the initial species simulated, representing the species pool, which led to a better exploration of the parameter space and therefore to the possibility of finding the right combination of species coexisting for larger N (Miller et al., 2024).

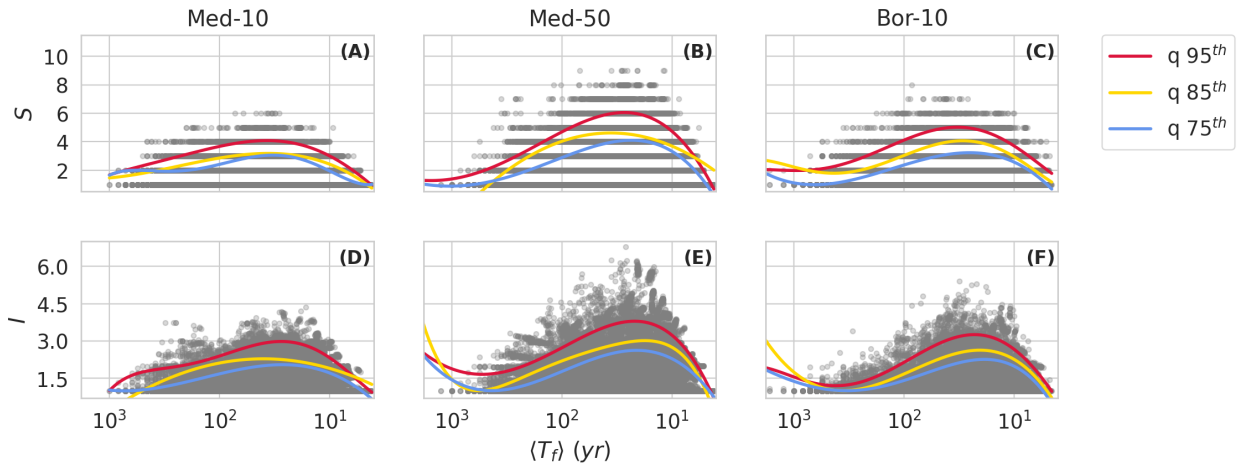

Figure 2: Compositional diversity plots as a function of fire return time for the Mediterranean communities with $N = 10$ (A, D) and $N = 50$ (B, E) initial simulated species, and for the Boreal communities of $N = 10$ (C, F) initially simulated species. Species Richness S (A, B, C) and Inverse Simpson Index I (D, E, F) are plotted versus average fire return time $\langle T_f \rangle$. The 95th (red), 85th (yellow) and 75th (blue) quantile regressions are reported for each plot, and their polynomial order is chosen based on the lowest AIC value (see Tables in Section D.1 in Appendix D. The x-axes are reversed to show the increment of the fire frequency, thus going from rare to frequent fires, in logarithmic scale.

Functional Richness F_R (fig. 3, top panels) also exhibited few communities with large maxima and several communities with intermediate-large values at intermediate-high fire return times for all community types. Maxima were especially pronounced in the Mediterranean communities. However, several of the quantile curves did not show the characteristic hump shape: the

95th quantile regression of the Med-10 and Med-50 communities, as well as the 85th quantile regression of the Bor-10 communities, decreased linearly towards lower fire frequency regimes. In addition, other regression fits were constant along the fire gradient or had shallow curvatures, namely the 75th quantile regression of the Med-10 and Bor-10 communities.

Functional Divergence F_D (fig. 3, bottom panels) instead showed maxima occurring at intermediate-high and high fire frequency for all ecosystems. Specifically, the quantile regression curves for the Med-10 community types peaked at intermediate disturbances and decreased towards higher and lower fire frequencies. The Med-50 and Bor-10 community types showed hump-shaped 75th and 85th quantile regression curves, while the 95th curve decreased monotonically towards lower fire return time, supporting the homogeneous pattern of diversity across fire return times suggested by the scatterplot.

Unlike compositional diversity indicators, the highest values of Functional Richness and Divergence were observed for the Med-10 communities (respectively 0.09 and 0.77), followed closely by the Med-50 (respectively 0.06 and 0.68) and the Bor-10 (respectively 0.05 and 0.79) communities. This indicated that the simulations reproducing the Boreal Forest species resulted in communities composed of plants that were functionally more similar than those in the Mediterranean Forest, given the same number of initial species. This is likely due to the parameterization, as the sampling ranges of C and M of the Boreal ecosystems were narrower than those of the Mediterranean ecosystems (fig. A1), possibly reflecting the differences observed between these ecosystems (Ordonez and Svenning, 2015, 2017; Padulles Cubino, 2023).

Comparing fig. 3 with fig. 2, we note that the quantile regression curves corresponding to functional diversity exhibited more dissimilarity between community types and metrics as compared to the compositional diversity curves. We also note that functional richness exhibited an elevated number of communities with low diversity values compared to the other biodiversity indicators. This was mainly due to the geometric dependency of F_R on S, as in the 5-dimensional parameter space, communities with species richness $S < 5$ created hyperplanes rather than hypervolumes, whose volume was equal to or close to 0. Finally, it is worth mentioning that the

sharp and increasing trend of some of the fit lines at low fire frequency (high fire return time, fig. 2 e and f, fig. 3 b, d, e and f) is not relevant, given it was caused by few isolated points which heavily influenced the shape of the curve fit.

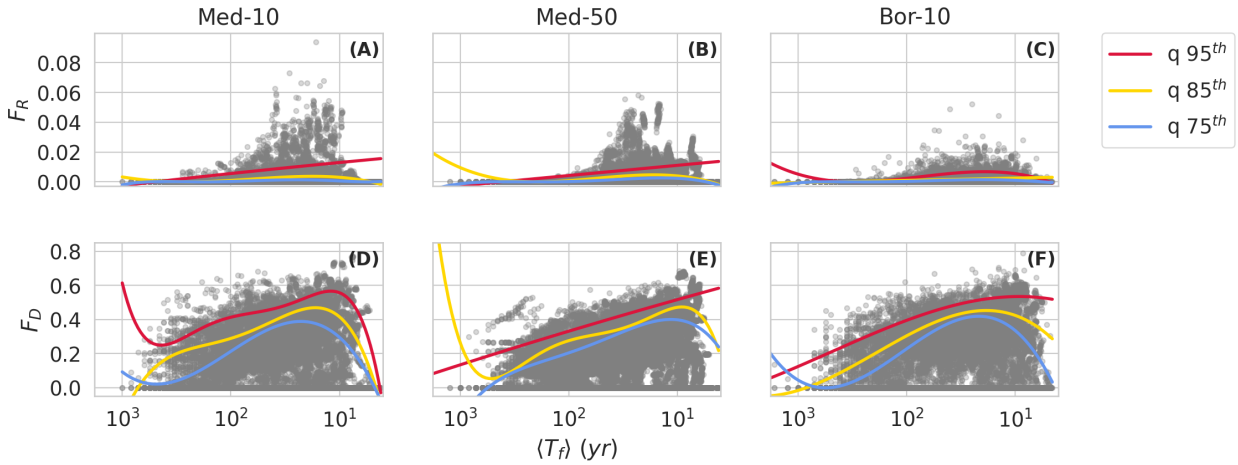

Figure 3: Functional diversity plots over fire frequency for the Mediterranean communities with $N = 10$ (A, D), $N = 50$ (B, E), and for the Boreal communities with $N = 10$ (C, F) initial species. Functional Richness F_R (A, B, C) and Functional Divergence F_D (D, E, F) based on the average plant cover are plotted versus average fire return time $\langle T_f \rangle$. The 95th (red), 85th (yellow) and 75th (blue) quantile regressions are reported for each plot, and their polynomial order is chosen based on the lowest AIC value (see tables D7-D12 in section D.2 in Appendix D). Note that the x-axes are reversed to show the increment of the fire frequency as in fig. 2.

To answer the third research question, we analyzed whether a larger number of coexisting plant species was associated with a larger variety of functional strategies (as captured by our model parameters). All biodiversity indicators positively and significantly correlated with each other in the different community types (see Appendix E), with the strongest correlations found between indicators of the same kind (compositional and functional). Conversely, the correlations of Species Richness with the two functional diversity indicators were weaker, with $r < 0.5$ in all the community types. Indeed, the maxima of functional diversity are not observed at the maximum values of specific richness (fig. 4), showing that the communities with the largest

number of species are not those with the greatest functional diversity. This suggests that, in the presence of fire, some level of similarity between species allows for a greater number of coexisting species.

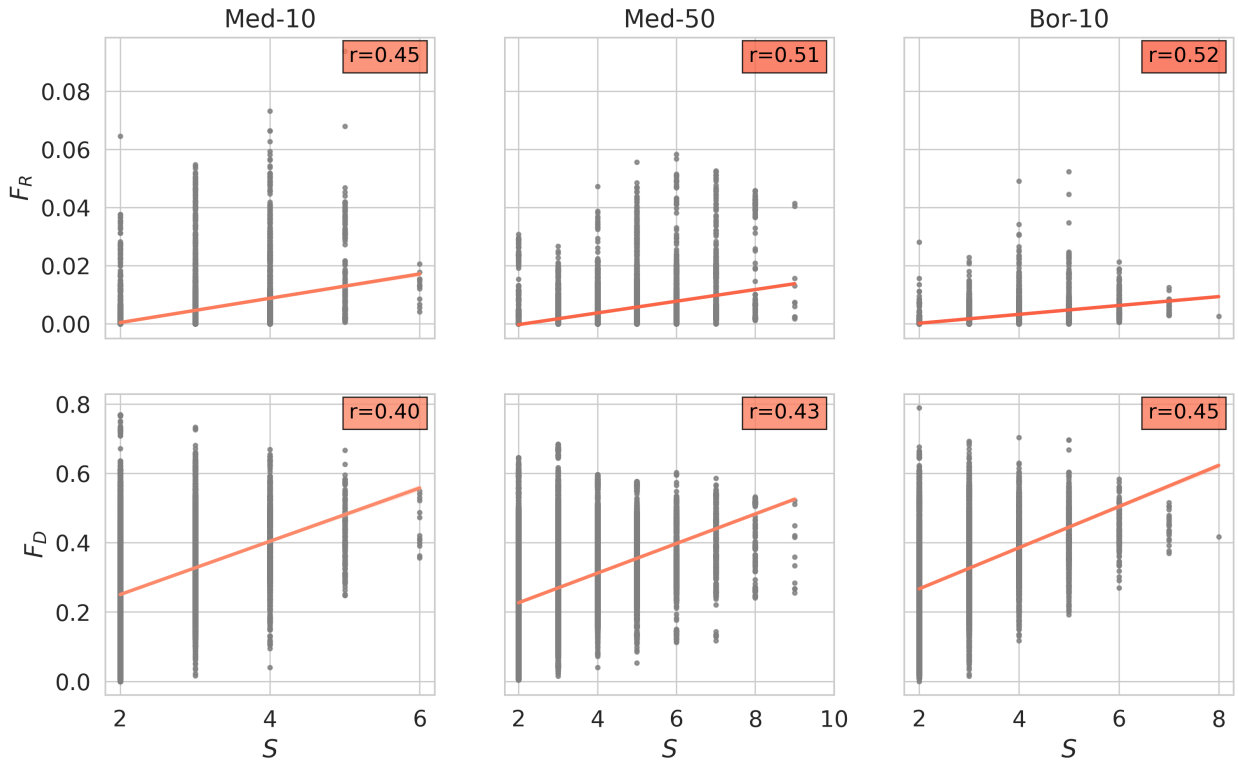

Figure 4: Functional Richness (top panels) and Functional Divergence (bottom panels) as a function of Species Richness, for: Mediterranean $N = 10$ (left panels); Mediterranean $N = 50$ (central panels); Boreal $N = 10$ (right panels). A linear regression line and the Pearson Correlation Coefficient r are reported for each panel. All the Pearson Correlation Coefficients reported resulted in significant correlation ($p < 0.05$).

Discussion

Our model results showed that, for both Mediterranean and Boreal fire-prone ecosystems, plant diversity peaked at medium fire frequencies and decreased towards the extreme of the fire re-

turn time gradient, similarly to earlier observations (Graham and Duda, 2011; Huston, 1994, 2014; Willig and Presley, 2018). While the biodiversity indicators analyzed (Species Richness, Inverse Simpson Index, Functional Richness and Divergence) were quite scattered when plotted as a function of fire return time, their top quantiles followed a hump-shaped curve as a function of fire return time. Specifically, compositional and functional diversity were, in most cases, higher in the simulations of plant communities prone to fires, as compared to simulations of the same set of species without fires. Furthermore, the highest plant community diversity occurred at intermediate fire frequencies, while less diverse communities were observed towards the extremes of the fire frequency gradient. Yet, interestingly, the two types of diversity did not peak in the same communities.

Fires tended to increase diversity, as observed by comparing the simulated communities obtained with and without fires. Furthermore, the highest levels of diversity were at intermediate values of fire frequency, but closer to the frequent end. This is consistent with the high biodiversity reported for fire-prone systems (He et al., 2019; Pausas and Ribeiro, 2017) and their tendency to maintain greater diversity under frequent burning conditions than under fire exclusion conditions (Pellegrini et al., 2023). We found the lowest biodiversity levels in low-frequency fire systems, where single species survived alone, similarly to real ecosystems dominated by late-successional species (e.g. Amici et al., 2013).

Our results thus followed the predictions of the Intermediate Disturbance Hypothesis. Mixed evidence has been reported for the IDH in general, as it fails to describe numerous empirical and theoretical results (Mackey and Currie, 2001), and has been criticized theoretically for a lack of appropriate mechanistic explanation behind the expected pattern (Fox, 2013). Notwithstanding, the IDH has been observed for fire-prone plant communities along a fire frequency gradient, although not in all instances (e.g. He et al., 2019; Pellegrini et al., 2023). The broader consensus on the IDH in fire-prone plant communities might be related to the vegetation-fire feedback, which is included in our model and is very relevant in real communities (e.g. Baudena et al., 2015; Pausas and Dantas, 2017; Rohde, 2013). In a recent paper with a model rather similar

to ours (Liao et al., 2022, based on the same competition-colonization equations and including fires as pulse disturbances), the IDH was not observed for plant compositional diversity. This difference possibly arises because in Liao et al. (2022) all the species were assumed to be affected to the same extend by fires — that is, the fire response was set equal for all species —, or because fires were represented as deterministic events, without including any vegetation-fire feedback. This latter explanation seems to be supported by an experiment we performed with a simplified version of our model, where we excluded the fire-vegetation feedback (by including stochastic fires with a fixed return time). The simulations did not display a maximum nor a hump shape for diversity indices, but, similarly to Liao et al. (2022), a multimodal relationship emerged when plotting data for specific communities along an imposed fire frequency gradient (see fig. F1 in Section F of Supplementary Material). Given the importance of the fire-vegetation feedback for different ecosystems (Pausas and Dantas, 2017), due to the effects of vegetation flammability on fire spread and the importance of the different post-fire regrowth strategies (Archibald et al., 2018; Harrison et al., 2021; Pausas and Verdú, 2008; Simpson et al., 2022) our results are likely to represent a key feature of many fire ecosystems.

A decoupling between compositional and functional diversity, similar to what observed in empirical studies in different biomes (Mirabel et al., 2020; Navarro-Cano et al., 2024; Pellegrini et al., 2023), emerged in our simulations: high levels of compositional and functional biodiversity are not observed in the same plant communities, although for both metrics the peaks occur at similar fire frequencies. This suggests that species that coexist in fire-prone ecosystems are not necessarily very different and might in fact share some characteristics, as fire selects these traits, being a strong community assembly process, as previously suggested by Pausas and Verdú (2008): for example, species might have a comparable growth rate and similar performance in fire response, enabling them to survive the same fire regime.

Our approach allowed us to make a general statement about the fire-diversity relationship by examining different parameterized ecosystems and considering different possible species pools associated with their self-sustained fire regime. We simulated the Mediterranean with a much

larger species pool than the Boreal ecosystems. The model could reproduce well the higher functional richness of the Mediterranean with respect to the Boreal ecosystems. However, species richness of the Mediterranean communities was smaller than what was expected from the observed plant diversity in the Mediterranean Basin biome (Cowling et al., 1996; Myers et al., 2000). This might be due to the fact that our parameterization, following Baudena et al. (2020), encompassed a parameter range for growth rates and mortalities that represents a variety of life forms, spanning from perennial grasses to late successional trees, but excluded annuals. This is a limitation of our approach when trying to represent Mediterranean communities, as annual plants are relevant in the Mediterranean ecosystems (Poppenwimer et al., 2023). Yet, given that we explored different biomes, characterized by very different parameter values and model behaviors (Magnani et al., 2023), we do expect that an inclusion of annual plants in the model for the Mediterranean ecosystem would lead to similar results as currently shown for diversity and fire regime. The relatively low values of species richness in the Mediterranean ecosystem might also be due to an undersampling of the simulated communities, since, despite the large number of simulations performed, only a portion of the possible parameter combination was explored, given the large dimensionality of the parameter space, especially for the simulations with 50 initial species.

At present, it is still unclear which model feature or plant characteristic let the hump-shaped distribution emerge in the model dynamics; more investigation could show for example which types of plant functional responses or characteristics of the initial species set (representing the species pool) are necessary for the final communities to be more or less diverse. Notwithstanding, the present study underlines the importance of fires for biodiversity in fire-prone ecosystems. In particular, we show that the fire-vegetation feedback, due to fire-related plant traits that determine plant flammability and the ability to re-grow after fires, is determinant not only for ecosystem resilience (Baudena et al., 2020; Magnani et al., 2023) but also for ecosystem compositional and functional diversity.

The connection between fires and biodiversity is very relevant also from management per-

spective, for example in relation to fire suppression or prescription strategies (e.g. Puig-Gironès et al., 2025). More generally, to predict the fate of ecosystems subject to global change, affecting biodiversity and wildfire regimes, and to support restoration action and management, modeling efforts should crucially include the vegetation-fire feedback, which, however, is often only partly represented in most global vegetation models (Hantson et al., 2016; Harrison et al., 2021; Kelley et al., 2014; Venevsky et al., 2019).

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Statement of Authorship

RDS and MB conceived the original idea; MT and GV developed the software (in Python and Fortran, respectively); GV led the model parametrization and simulations; MT led the analyses and visualization of results; RDS, MM and ME provided useful feedback during the analyses; MT, GV and MB wrote the original draft; MB supervised the work; All the authors contributed to reviewing and editing.

Data and Code Availability

The data shown in this paper were produced by model simulations. The simulation code and analysis methods for the reproduction of results presented here are available in the GitHub repository: `https://github.com/torrassam/Fire-Diversity.git`.

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