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A synthesis of the Devonian wildfire record: Implications for paleogeography, fossil flora, and paleoclimate

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ABSTRACT

The Devonian is known for the earliest dispersal of extensive wildfires, but the spatiotemporal diversification pattern and process have not been studied in detail. We synthesize a total of 65 global wildfire occurrences based on fossil charcoals and geochemical (biomarker) evidence from 10 paleogeographic areas across 10 time bins (Lochkovian–late Famennian). Stratigraphically, the highest number of wildfire occurrences is found in the Late Devonian, especially the late Famennian. Paleogeographically, Devonian wildfire evidence is highly concentrated in the eastern Euramerican region that consists of the Appalachian Basin, Avalonia, and Baltica along the Acadian landmass. These data collectively define a unique diversification pattern, here coined as the 'Famennian Wildfire Explosion' (FWE). This possible global wildfire spread, based on our diversity analysis of the plant fossil record in eastern Euramerica, is tightly corresponding to the paleogeographic distribution of lignophytes, but not to other common groups of Late Devonian woody plants (e.g., lycopodiopsids, spermatophytes, pteridophytes-monilophytes). Those lignophyte trees and shrubs include 34 species of Aneurophytales, Archaeopteridales, and Spermatophytes in the eastern Euramerican area that represent the primary forest component as the major fuel source of the FWE. By comparing our wildfire and fossil plant diversity with available paleoclimate data (e.g., global atmospheric oxygen level, paleohumidity), we suggest that the FWE in eastern Euramerica is unique due to a combination of occurrences (i) in a relatively low paleolatitudinal zone and (ii) in arid and warm temperate climate zones, but it shows (iii) a relatively weak correlation with the rapidly increasing atmospheric oxygen level.

1. Introduction

Wildfires can be devastating to various levels of biotic (e.g., vegetations, non-plant organisms) and abiotic (e.g., soils, water, atmosphere) components in terrestrial and aquatic ecosystems (Delcourt and Delcourt, 1988; Pyne et al., 1996; Bond and Keeley, 2005; Bowman et al., 2009; Flannigan et al., 2009; Scott, 2020). In modern ecology, the dynamic nature of wildfires has been considered essential in mediating the interactions between living organisms and surrounding environments (e.g., plant ecology, soil geochemistry, climate change) (Keddy, 2017). Although extensive data are available for modern wildfire studies, a limited quantity and quality of evidence are available to assess spatiotemporal distributions of Paleozoic paleowildfires. Following the earliest known wildfire in the latest Silurian (Glasspool et al., 2004), scattered paleowildfire occurrences have been known from Devonian rocks (Supplementary Fig. S1), which is in contrast to much more abundant evidence from the Carboniferous and Permian in the Paleozoic record (Scott and Jones, 1994; Scott and Glasspool, 2006; Scott, 2020).

Despite the scarce nature of Devonian wildfire evidence, three previous studies have attempted to evaluate the diversification pattern in the Paleozoic record (Table 1). Scott and Glasspool (2006) first compiled global data on paleowildfire occurrences and proposed three notable events around the Devonian Period: (i) the earliest known wildfire in the latest Silurian; (ii) the 'charcoal gap' (i.e., the scarce occurrence) throughout the Middle Devonian (i.e., also proposed by Algeo and Ingall, 2007), and (iii) 'the first tropical mires' (i.e., the first global diversity) under a wet tropical climate in the Early Mississippian. Following this benchmark study, Glasspool et al. (2015) and Lenton et al. (2016) conducted a further investigation on the Devonian wildfire history incorporating some additional data of paleowildfires with other relevant elements (e.g., plant diversity, atmospheric oxygen level). However, their interpretations on the Devonian wildfires are based on a

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Table 1
A summary of previous studies of Silurian–Devonian wildfire diversification.

Source	Sample size[a]	Reference count[b]	Data type[c]	Geographic setting	Time bins
Scott and Glasspool (2006)	9	9	Inert.	1 realm (globe); unspecified sites	7
Glasspool et al. (2015)	15	13	Inert.	1 realm (globe); unspecified sites	5
Lenton et al. (2016)	30	25	Inert. & Fossil	1 realm (globe); w/21 sites	8
This study	58	45	Inert., Fossil, & Bio	10 areas; w/56 sites	11

[a] A total number of data entries.
[b] A total number of publications (references) for data entries.
[c] *Inert*: inertinites (mostly microscopic size fossil charcoals) from rock layers (coal, shale, sandstone, etc.); *Fossil*: meso- and macroscopic size fossil charcoals associated with plant fossils; *Bio*: biomarker.

limited sample size: nine, 15, and 30 occurrences (studied sites or geologic units) in Scott and Glasspool (2006), Glasspool et al. (2015), and Lenton et al. (2016), respectively (Table 1). Moreover, their studies on the wildfire diversification are based on a compilation of global data with a broad geologic time setting (Age/Stage-level). Thus, many questions and uncertainties have remained for understandings of the early paleowildfire evolution.

As an important part of paleowildfire studies, the data source and credibility are essential particularly for identifying paleowildfire evidence. The three Devonian wildfire studies (Scott and Glasspool, 2006; Glasspool et al., 2015; Lenton et al., 2016) primarily utilized data of inertinites (i.e., microscopic-size fossil charcoals) from coal-bearing layers. Other types of paleowildfire remains, however, can be available and also important for the Devonian record. For example, larger-sized fossil charcoals, especially mesoscopic and macroscopic remains, that are categorized as the inertinite group macerals (ICCP, 2001; Scott and Glasspool, 2007; (Scott, 1989)Scott, 2010; Tanner and Lucas, 2016), are available. Also, biomarker-based geochemical evidence, specifically pyrogenic polycyclic aromatic hydrocarbons (PAHs), has been recently used to detect Paleozoic paleowildfire signals in various types of sedimentary rocks (e.g., Marynowski and Filipiak, 2007; Shen et al., 2011; Kaiho et al., 2013, 2021; Lu, 2020). Moreover, a considerable number of studies have recently reported new evidence of paleowildfires (i.e., fossil charcoals and biomarkers) from not only non-coal bearing layers but also other types of sedimentary rocks (e.g., shales, sandstones). Those new Devonian data can provide a newly revised overview of the Devonian wildfire evolution across a specific time (e.g., geologic unit-level) and space (e.g., paleogeographic provinces/regions).

The timing of the first global wildfire expansion has been suggested repeatedly to correspond to that of the early forestation during the Late Devonian (e.g., Knoll, 1984; Driese and Mora, 2001; Algeo and Ingall, 2007; Algeo and Scheckler, 2010; Lu et al., 2019; Lu, 2020). A few studies attempted to combine and compare global trends of vascular plant and paleowildfire occurrences. Lenton et al. (2016) shows a coevolutionary pattern between the wildfire distribution and trilete spore diversity through the late Silurian to the Devonian transition. Scott and Glasspool (2006) and Glasspool et al. (2015) proposed an increasing trend of the estimated wildfire intensity synchronizing with the vascular plant evolution through the Middle Devonian to the Early Permian. Those previous studies used the relative timing for evaluating the vascular plant diversity through the Devonian, yet robust analyses based on specified time (stratigraphic units or geologic ages), space (paleogeographic regions), and plant taxa (family, genus, or species level) have not been conducted. Without incorporating these kinds of spatiotemporal data, identifying a specific type of evolutionary relationship (e.g., coevolution, divergent, parallel) between wildfire and vascular plant diversities can be problematic.

The primary purpose of this study is to review and revise the evolutionary pattern and process of the wildfire diversification along with the vascular plant diversity throughout the Devonian, incorporating newly available data. We synthesize global Devonian wildfire occurrences to assess (i) the paleogeographic and (ii) stratigraphic distribution and determine timings of a specific diversity peak(s), dispersal patterns, and potential hotspots and high frequent times. We also compare selected ecological components (e.g., fuel source, environmental conditions, climate types) of Devonian and modern wildfires. This approach may allow investigating unique features of the early wildfire evolution that may reflect transitions of the woody plant diversity (i.e., first forestation) and certain paleoclimate conditions.

To better understand the dynamic interaction between Devonian wildfires and the early forestation, we also synthesize the diversity data of vascular plant taxa from a selected paleogeographic region (i.e., eastern Euramerica). A tremendous amount of Devonian plant fossils that have been discovered across the globe give a sufficient amount of information on the early vascular plant evolution. Among various tracheophyte lineages that first appeared and had diversified through the Devonian, the first shrubs and trees are known from the latest Middle Devonian (Matten, 1974; Stein et al., 2007, 2012). Many of those early vascular plants are characterized by newly evolved wood tissues (i.e., the secondary xylem), true leaves, a deeply penetrating root system, and a gigantic overall size (Chaloner and Sheerin, 1979; Algeo and Scheckler, 2010; Kenrick and Crane, 1997; Hao and Xue, 2013; Shekhar et al., 2019; Stein et al., 2020). These newly evolved characteristics allow them to invade to new habitats (e.g., inland, semi-arid environments) and disperse to a larger geographic region, manifested as the first afforestation process in the late Middle to the latest Late Devonian (Knoll, 1984; Decombeix et al., 2011; Le Hir et al., 2011; Cascales-Miñana and Meyer-Berthaud, 2015; Xiong et al., 2013; Zheng et al., 2020). The early forestation is, thus, hypothetically the strongest candidate for the major fuel source. Multiple lineages, such as lycopodiopsids, paratracheophytes, pteropsids, and lignophytes (i.e., including many taxa referred to as the paraphyletic progymnosperms), are suggested as the major fuel source of wildfires (Rowe and Jones, 2000; Algeo and Ingall, 2007), but direct paleowildfire evidence that shows the co-occurrence of identifiable plant fossils (e.g., partially burned tree trunk and branches) is scarce. The question, thus, arises whether the Devonian wildfire diversification synchronizes with certain plant taxa or vegetation types that are highly flammable in a specific paleogeographic region(s) through a certain time.

Using the diversity data on Devonian wildfires and vascular plants, we will first discuss potential preservational and sampling biases (e.g., rock types, depositional environments) that may influence our interpretations on the Devonian wildfire dataset. Then, the significance of some key Devonian paleoclimate conditions that may influence wildfire evolution, particularly focusing on the atmospheric oxygen level (pO_2) and paleo-humidity will be undermined based on comparisons with modern wildfires.

2. Geological setting

To quantify paleowildfire occurrences, the Devonian Period (419.2–358.9 Ma) with seven stages were sub-grouped into 10 time bins (D1 to D10) (Table 2). Of the seven Devonian stages, the Emsian, Frasnian, and Famennian have a relatively long duration (i.e., over a 10 million-year duration). The three stages were split into two subdivisions, following the Subcommission on Devonian Stratigraphy (SDS), as shown

Table 2
Ten time bins of the Devonian used for this study.

10 bins	Devonian epoch	Stage	Duration (Myr)	Range (Ma)
Devonian 10	Late	Upper Famennian	6.65	365.5–358.9
Devonian 9	Late	Lower Famennian	6.65	372.2–365.55
Devonian 8	Late	Upper Frasnian	5.25	377.45–372.2
Devonian 7	Late	Lower Frasnian	5.25	382.7–377.45
Devonian 6	Middle	Givetian	5.00	387.7–382.7
Devonian 5	Middle	Eifelian	5.60	393.3–387.7
Devonian 4	Early	Upper Emsian	7.15	400.45–393.3
Devonian 3	Early	Lower Emsian	7.15	407.6–400.45
Devonian 2	Early	Pragian	3.20	410.8–407.6
Devonian 1	Early	Lochkovian	8.40	419.2–410.8

Mid-point (median) is used for a subdivision (early and late) of the Emsian, Frasnian, and Famennian.

in Becker et al. (2012). The subdivisions include the Early and Upper Emsian intervals (D3 and D4). The Frasnian has three subdivisions in the SDS system, but here we used the median point (i.e., approximately no. 5 or the *Palmatolepis jamieae* zone in the Standard Conodont Biozone during the Frasnian) to establish two time bins: early and late Frasnian (D7 and D8). The longest stage in the Devonian Period is the Famennian, which was divided into two time bins (early and late Famennian: Devonian 9 and 10) at the mid-point. The average duration of the 10 time bins is 6.03 million years with a range of 3.20 million (Devonian 2: Pragian) to 8.40 million (Devonian 1: Lochkovian) years. Using the 10 time bins, we quantified wildfire occurrences and taxonomic counts of vascular plants, primarily based on geologic units (i.e., Formation and Member). For each occurrence, location (paleogeographic and current places), depositional setting (marine or terrestrial), general rock type (clastic, biochemical sedimentary, and metamorphic), specific rock types (various sedimentary rocks such as shale, siltstone, and sandstone were also recorded.

Ten Devonian paleogeographic areas, which are physically isolated by seas or identifiable landmass (e.g., realms, regions, provinces; Dowding and Ebach, 2019) are used for counting paleowildfire occurrences in this study (Fig. 1). Some regions represented marine basins (shallow or coastal marine paleoenvironments during the time while others were referred to as terrestrial. Of the ten paleogeographic regions, Siberia (eastern Russia) and Tarim (Xinjiang Province in northwestern China) were placed entirely in the Devonian Northern Hemisphere. The Euramerica was placed across the paleoequator. The eastern Euramerica consisted of six subdivisions: southern Appalachian Basin (including the present location of Kentucky, Ohio, Virginia, West Virginia, Tennessee, and Alabama in the U.S.A.), northern Appalachian Basin (e.g., New York and Pennsylvania in the U.S.A. and Quebec in Canada), Avalonia (the U. K., Belgium, Germany, Poland, and New Brunswick in Canada), and Baltica (e.g., Norway, Ukraine, western Russia). The central to western Euramerica consisted of northcentral Laurentia (e.g., Nunavut in Canada) and western Laurentia (e.g., Oklahoma in the U.S.A.). The composition of landmasses referred to as Gondwana and China changed through the Devonian. Three regions were strictly used for evaluating the paleowildfire distribution, including Gondwana (Tunisia and Libya in Africa and Australia), South China (e.g., Yunnan Province), and Tarim (e.g., Xinjiang Province). Paleolatitudes of wildfire occurrences were estimated based on three paleogeographic maps by three maps by Torsvic and Cocks (2016) (Early, Middle, and Late Devonian: 410 Mya, 390 Mya, and 370 Mya) and eight maps by Scotese (2014) including 413.6 Mya (for Devonian 1), 409.1 Mya (for Devonian 2), 402.3 Mya (for Devonian 3 and Devonian 4), 394.3 Mya (for Devonian 5), 388.2 Mya (for Devonian 6), 379.9 Mya (for Devonian 7 and Devonian 8), 370.3 Mya (for Devonian 9), and 359.2 Mya (for Devonian 10).

In our wildfire data matrix of the 10 paleogeographic areas across the 10 time bins, hiatuses exist due to disconformity and nonconformity. Because missing time and/or space can create a strong bias for quantifying wildfire and land plant distributions, the hiatus record was examined.

3. Materials and methods

3.1. Silurian–Devonian wildfire data

Identifying and selecting consistent and reliable Devonian wildfire data is the most crucial step for building the database for this study. Since no publicly accessible database for the Paleozoic–Mesozoic wildfire record exists in the literature and online, we compiled data solely from publications in peer-reviewed journals (Supplementary Table S2). Unpublished data (e.g., personal webpage) and personal materials were entirely excluded. For a literature search, we used the following keywords, 'Devonian wildfire', 'fossil charcoal', 'inertinite', 'fusain', 'fusinite', and/or 'PAH' (pyrogenic polycyclic aromatic hydrocarbons), in Google Scholar and the Web of Science. Original research articles were further checked by a cross-reference in original journal websites

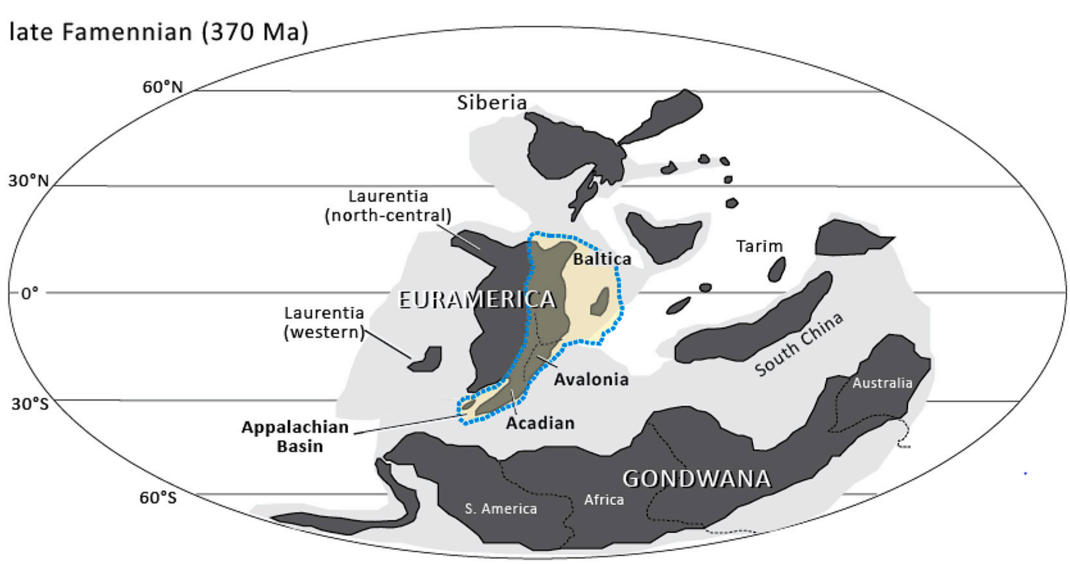

Fig. 1. Devonian paleogeography for this study. The map (Late Devonian: 370 Ma) is redrawn based on Scotese (2014) and Golonka (2020). Blue dotted line with a yellow polygon represents eastern Euramerica, which shows the main focus of this study. Dark grey indicates landmass. Light grey shows a shallow marine shelf. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and some major search engines (e.g., ScienceDirect, JSTOOR). All literature search was conducted by the end of March 2020.

The original datasets of the three studies of the Devonian wildfire evolution (i.e., Scott and Glasspool, 2006; Glasspool et al., 2015) and Lenton et al. (2016) were also reviewed and incorporated in this study (Table 1). To evaluate the credibility of fossil charcoal evidence in those publications, anatomical characteristics, charcoal reflectance, and preservation in original articles were checked and evaluated before included in our database. The standardized guideline (Scott, 2000, 2010, 2020) and the classification (Scott and Glasspool, 2007) of fossil charcoals were used to minimize the possibility of including false wildfire evidence, such as various grades of coals, petrified plant materials, funginites, and other non-inertinite macerals (e.g., alginites).

Two types of Devonian wildfire evidence were recorded separately for our database: fossil charcoals and biomarkers (PAHs) (Supplementary Fig. S1). Fossil charcoals are readily recognized as brittle, black materials with a silky luster feature (Chaloner, 1989; Scott, 2010). Many fossil charcoals are broadly assigned to the inertinite-group macerals (e.g., fusinites, semifusinites) (Scott and Glasspool, 2007; Scott, 2010). Inertinites were the main data source for Devonian fossil charcoals in the three previous studies (Scott and Glasspool, 2006; Glasspool et al., 2015; Lenton et al., 2016) (Table 1). Inertinites are generally preserved in coal or peat as microscopic-size fragments with evident anatomical structures (esp., cell walls) and high reflectance (ICCP, 2001; Scott and Glasspool, 2007; Scott, 2010).

Preservational settings of inertinites (e.g., rock types) were not provided in the Devonian dataset of Scott et al. (2006: Fig. 1) and Glasspool et al. (2015: table S1). Lenton et al. (2016), however, categorized two types of fossil charcoals in their dataset: (i) isolated inertinite fragments from various types of sedimentary rock layers (i.e., ‘Coal’, ‘Coaly shale’, and ‘Black shale’) and (ii) larger fragments associated with actual plant fossils (i.e., ‘Fossil’) (listed in their table S1). We adapted their approach (Lenton et al., 2016) to quantify Devonian wildfire occurrences in the two types of fossil charcoal data: inertinite-based (Inert.) and fossil plant remain-associated (Fossil) evidence, as indicated in Table 1.

To separate the two types of fossil charcoal data, the physical size of preserved material can be essential. The fossil charcoal type generally includes three size categories: microscopic (i.e., generally less than 180 μm), mesoscopic (i.e., 180 μm to 1.0 mm), and macroscopic (greater than 1.0 mm) (Jasper et al., 2013; Scott, 2010; Scott, 2020). Microscopic fossil charcoals are referred to as ‘inertinites’ in some studies (e.g., Scott and Glasspool, 2006; Glasspool et al., 2015; Lenton et al., 2016) (Table 1). In this study, the charcoal size was recorded in two categories when the information was available, ‘microscopic’ (referring to inertinite-type) and ‘meso- & macroscopic’ (referring to non-inertinite-type). The larger-sized group is generally associated with actual fossil plant remains (Fossil). Small microscopic fragments (inertinites) can be preserved in any condition although most of them indicate non-association with plant fossils.

It should be noted that fossil charcoal identification in the publications may not be consistent, and different methods can be employed, including (i) a simple statement without any supportive data, (ii) detailed physical descriptions (by naked eye observations) with a supportive figure(s), and (iii) a description and presentation of microscopic-level structures (using reflective light microscopy or SEM) (e.g., Edwards and Axe, 2004; Rimmer et al., 2015). We gathered all published data (a summary in Supplementary Table S1 and raw data listed in Supplementary Table S2) but did not simply take face values from all literature sources. Data sources in the first category were excluded for further data analyses, such as inertinites reported from the Middle Devonian gneiss unit of Germany (Pflug and Prössl, 1989; Pflug and Prössl, 1991) and a very brief statement of wildfire from the Givetian Haikou Formation of southwestern China (Rimmer et al., 2015; Song et al., 2015).

The other type of wildfire evidence comes from PAHs, which are widely distributed organic compounds with petrogenic and pyrogenic origins (Killops and Massoud, 1992; Yunnker et al., 2002). Among different types of PAHs, such as the pyrolytic PAHs (e.g., pyrene, benzofluoranthenes, benzo[*e*]pyrene, benzo[*ghi*]perylene, coronene) are thought to be associated with the combustion of woods that can be linked to paleowildfires (Jiang et al., 1998). In this study, we included all available data of pyrogenic PAHs from Devonian rocks.

Using data from both fossil charcoals and biomarkers, wildfire occurrences were scored based on the 10 time bins. The age data were determined by stratigraphy of the original geological unit (mostly Formation, but Member for a few cases; indicated in Supplementary Table S2). Although most study sites (sections or outcrops) usually produced paleowildfire evidence from a single layer, a few studies showed multiples across consecutive strata or even geological units. When wildfire evidence was collected across successive members of a single formation, two occurrences were scored. When no fire evidence was reported, we scored ‘0’ for each of the 10 time bines and the 10 paleogeographic areas. For hiatus-bearing time bins (i.e., physically missing strata and rocks in time and space), we scored ‘H’ with a note.

3.2. Vascular plant data

Data of the Devonian vascular plant record from the eastern Euramerica (a summary in Supplementary Table S4 and raw data in Supplementary Table S6) were originally adopted and further developed from a database of Lu et al. (2019). Their dataset included data of 29 genera and 62 species from 14 states/provinces of the eastern U.S.A and Canada (i.e., Acadian landmass excluding Baltica and Avalonia) to determine paleogeographic distribution at the Stage/Age-level time scale. For further utilizing this dataset, we also incorporated extensive additional data from recent publications (i.e., listed in Supplementary Table S6) and sorted data at the species level with a finer time scale (the 10 Devonian time bins: Table 2) from the entire eastern Euramerica. Our dataset also incorporated several studies of the Devonian plant diversity, including Cascales-Miñana and Meyer-Berthaud (2015), Xiong et al. (2013), Hao and Xue (2013), Xue et al. (2015), Barrett (2016), and Gerrienne et al. (2016), to extract some data of occurrences or to check the status of some taxa.

To check the systematics of the higher-level phylogenetic relationship of Devonian vascular plants, Kenrick and Crane (1997) and Crane et al. (2004) were primarily used. For determining the generic and specific level taxonomy, we generally followed information on the Paleobiology Database (http://fossilworks.org accessed in October 2019) and the International Fossil Plant Names Index (http://www.fossilplants.info/index.htm).

All species and genera within the vascular plant clade, Tracheophytes, were identified in six taxonomic groups: (i) paratracheophytes (including stem and basal tracheophytes), (ii) stem lycopodiopsids, (iii) derived lycopodiopsids, (iv) basal euphyllophytes (including the paraphyletic trimerophytales), (v) basal lignophytes (including the paraphyletic progymnosperms and spermatophytes), and (vi) the Pteridophytes-Monilophyta lineage (i.e., a single monophyletic clade). Some selected representatives for each group are listed in Table 3. Species and genera were counted separately in the10 time bins and 10 paleogeographic areas.

Alpha taxonomy for some Devonian vascular plant taxa can be controversial or problematic. For example, a considerably large number of species are assigned to *Archaeopteris* and *Callixylon* although the two genera are likely a synonymy (Beck, 1960). To date, no method is available for synonymizing the two taxa at the species level. Also, many other Devonian taxa are established based on limited anatomical parts (leaf, trunk, etc.). We, thus, analyzed them separately and inclusively. Taxa with an uncertain taxonomic affinity (i.e., not listed in this study), stratigraphic age, and/or locality (at least, province- or state-level) were excluded from this study.

Table 3
Six groups of Devonian vascular plants for this study.

Groups	Key higher taxa	Remarks
pa: Paratracheophytes	Cooksonioids; Rhyniopsida	– Basal vascular plants (tracheophytes)
ly-1: stem lycopodiopsids	Barinophytales; Gossilingiales; Sawdoniales; Zosterophyllales	– Their phylogenetic relationship is largely unsolved. A few may be assigned to basal taxa within Lycopodiopsida.
ly-2: Lycopodiopsida (basal & derived taxa)	Drepanophycales; Lepidodendrales; Lycopsida	– Including basal to derived taxa within the clade Lycopodiopsida.
eup: basal euphyllophytes & stem lignophytes	Psilophytopsida;	– Stem and basal taxa assigned to Euphyllophytina, including ancestry lignophytes
lig: Lignophytes (derived taxa)	Aneurophytales; Archaeopteridales; Spermatophyta	– Including taxa assigned to Spermatophytes and the paraphyletic progymnosperms
P-M: Pteridophyta/ Monilophyta	Cladoxylopsida; Equisetophyta; Filicopsida; Rhacophytales	– The ingroup relationship is largely unsolved; Pteridophyta and Monilophyta are exchangeable but likely the same monophyletic clade

They are common in eastern Euramerica (Lu et al., 2019). Phylogenetic affinities are determined based on Kenrick and Crane (1997) and Gerrienne et al. (2016).

3.3. Taxonomic rates and diversity parameters of Devonian vascular plants

Origination percentages (the species count of the least appearances/ that of the total appearance*100%) are a commonly used parameter to assess the diversity magnitude for a wide range of fossil taxa (e.g., Ikejiri et al., 2020). The origination percentages of vascular plant species from eastern Euramerica were calculated through the 10 time bins of the Devonian (Table 2) for two datasets separately: including all singletons (i.e., species occurrences only in a single unit) and excluding singletons (i.e., occurrences in more than one unit: boundary crossers) (Foote, 2000a, 2007). Singleton occurrences can be theoretically a strong source of biases for diversity analyses in the fossil record (Foote, 2000a). However, Paleozoic plants are known to exhibit a high number of singleton taxa, which was suggested to reflect the true condition (Cascales-Miñana and Diez, 2012). Moreover, another study demonstrated a relatively weak effect of sampling variations (e.g., inconsistent samplings in locations, rock types, and ages, researchers' interests) on the Devonian vascular plant record (Raymond and Metz, 1995).

We calculated three other types of commonly used taxonomic rates: (i) proportional origination for species within a single interval (PO), (ii) PO per million years (PO/myL), and (iii) per-capita origination rate (p) for species within a time bin but excluding singletons (following Foote, 2000b). The latter two rates incorporate the time data (duration) while the first one does not. For measuring diversity, we compared two indices, the standing diversity (i.e., (extinct + originate count)/2; Cascales-Miñana and Diez, 2012) and the Dominance Index (i.e., 1 − Simpson's H Index), for each of the six vascular plant groups across the 10 time bins.

3.4. Statistical analyses

A rarefaction curve was calculated to evaluate the quantity of sampling efforts in the Devonian record, using the PAST Version 2.08 (Hammer et al., 2001). The rarefaction is commonly used for the fossil and paleontological records to assess relative fossil richness through a stratigraphic interval along with sampling effort (Raup, 1975, 1991). This method compensates for the effects of sampling size on fossil richness and, thus, is used to address the issue of incompleteness that is intrinsic to the fossil record (Foote and Miller, 2007). It can be applied to various taxonomic levels although species and genus are the two most commonly applied taxonomic levels (e.g., Ikejiri et al., 2020). In this study, we utilized the rarefaction curve to assess wildfire occurrences relative to the sampling effort (i.e., the count of geologic units: formations). This allows determining whether observations (sampling efforts) sufficient enough to generate a reasonable estimate of the Devonian wildfire occurrences. When the curve reaches a horizontal asymptote, it can be inferred that the observations are adequate to generate a robust estimate.

Paleolatitudinal distribution of the Devonian wildfires was also quantified to assess if wildfire evidence was more abundant in particular paleolatitudes. To determine paleolatitudinal values for each occurrence, five Devonian paleogeographic maps by Scotese (2014) were used. The five maps included (1) early Early Devonian (Lochkovian), (2) late Early Devonian (Emsian), (3) Middle Devonian, (4) early Late Devonian (early Frasnian), and (5) late Late Devonian (late Famennian). A difference in the topology of landmasses between the earliest and latest Devonian maps showed a gap of approximately 10 latitudinal degrees. Then, the Shapiro-Wilk test was first applied to determine the normality of the wildfire data along paleolatitudes. Subsequently, Bootstrap Resampling method was used to determine the overall structure of the population relative to the paleolatitudes (0–65 degrees in the Devonian southern and northern hemispheres) by random sampling (i.e., replicated by 500 times) and estimated confidence intervals. The Bootstrap Resampling method is suitable for analyzing relatively small-sized datasets in various fields of science, and it has been applied to the paleontological record (Kowalewski and Novack-Gottshall, 2010).

For determining the magnitude of correlation among the wildfire occurrences, rock types, depositional settings, atmospheric oxygen levels, and plant species counts (using a 95% CI), Kendall's τ test was employed to determine whether two curves rise and fall concurrently (Fröbisch, 2013).

Principal Component Analysis (PCA) is generally used to summarize and visualize a multivariate dataset and delineate the direction and strength of correlations among involving variables. We ran the PCA to determine the intercorrelation and strength of the wildfire diversity (frequency) with possible controlling factors including plant diversity, rock volume, and the atmospheric oxygen level. All data were standardized prior to run the PCA analysis and grouped into the late Silurian–10 Devonian time bins.

4. Results

4.1. Silurian–Devonian wildfire record in the geological context

Of the 10 Devonian time-bins across the 10 paleogeographic areas, only three evident (and two possible additional) occasions showed physically missing rock-intervals due to disconformities (Table 4). Those hiatus-bearing intervals included Devonian 1 (Lochkovian) in the northern Appalachian Basis, Devonian 3 (early Emsian) in western Laurentia, and Devonian 7 (early Frasnian) in Tarim (northwestern China). The rest of the 97 entries had, at least, one geologic unit in time and space for examining possible wildfire evidence.

During the late Silurian (the Pridoli) to the latest Devonian (the end-Famennian), wildfires were observed in 36 geologic units (formations). In total, 65 occurrences of paleowildfire evidence (one Silurian and 64 Devonian) were found (summaries available in Table 5 and Supplementary Table S1; raw data listed in Supplementary Table S2). Those were based on 52 occurrences that consisted of the fossil charcoal (75.4% in the total) and 17 biomarker (PAHs) (24.6%) based paleowildfire evidence, including four of them for both types (i.e., the total of 69 including four duplicated cases for both types). These four studies that presented both fossil charcoal and geochemical data were from

Table 4
Hiatus occurrences in the rock record from late Silurian (Sil.) to Devonian 10 (D10).

Paleogeographic regions	Sil.	D1	D2	D3	D4	D5	D6	D7	D8	D9	D10
Appalachian Basin (southern)*	P	P	P	P	P	P	P	P	P	P	P
Appalachian Basin (northern)*	P	A	P	P	P	P	P	P	P	P	P
Avalonia*	P	P	P	P	P	P	P	P	P	P	P
Baltica*	A?	P	P	P	P	P	P	P	P	P	P
Laurentia (north central)	P?	P	P	P	P	P	P	P	P	P	P
Laurentia (western)	P	P	P	A	P	P	P?	P	P	P	P
Siberia	P?	P	P	P	P	P	P	P	P	P	P
South China	P	P	P	P	P	P	P	P	P	P	P
Tarim	P	A	P	P?	P	P	P	A	P	P	P
Africa	P	P	P	P	P	P	P	P	P	P	P
South America	P	P	P	P	P	P	P	P	P	P	P
Australia	P	P	P	P	P	P	P	P	P	P	P

A: absence (= hiatus); P: presence of a rock unit(s). Regions with an asterisk mark represent eastern Euramerica.

Table 5
Key sampling features for the 65 occurrences of Silurian–Devonian wildfires occurrences in this study.

Key features	Subtotal (n)	Category A	Category B	Category C
(i) Wildfire evidence types	69	Fossil charcoal: $n = 52$ (75.4%)	Biomarker: $n = 17$ (24.6%)	Both: $n = 4$ (5.8%)
(ii) Depositional settings	65	Marine: $n = 44$ (67.7%)	Terrestrial: $n = 21$ (32.3%)	NA
(iii) Rock type I	71	Clastic: $n = 64$ (90.1%)	Biochemical: $n = 6$ (8.5%)	Unknown: $n = 1$ (1.5%)
(iv) Rock type II	74	Shale: $n = 44$ (59.5%)	Non-shale: $n = 30$ (39.5%)	NA
		Sandstone + siltstone: $n = 25$	Limestone: $n = 4$	Coal bearing layer: $n = 13$

Key features		df	Chi-square	P (no assoc.)	Monte Carlo P
Evidence vs. Depo.	(i) vs (ii)	1	0.9691	0.3249	0.3488
Evidence vs. Rock I	(i) vs. (ii)	1	6.4954	0.011*	0.0142
Evidence vs. Rock II	(i) vs. (iv)	1	4.0926	0.0431*	0.0496
Depo vs. Rock I	(ii) vs. (iii)	1	11.868	0.001*	0.0007
Depo. vs. Rock II	(ii) vs. (iv)	1	1.0097	0.3150	0.3733
Rock I vs. Rock II	(iii) vs. (iv)	1	19.608	0.001*	0.001

Top: A summary of sample size for each category. *Bottom*: Results of the Chi-Square analysis. Raw data are listed in Supplementary Table S2. Asterisk mark indicates significantly different values ($P < 0.05$).

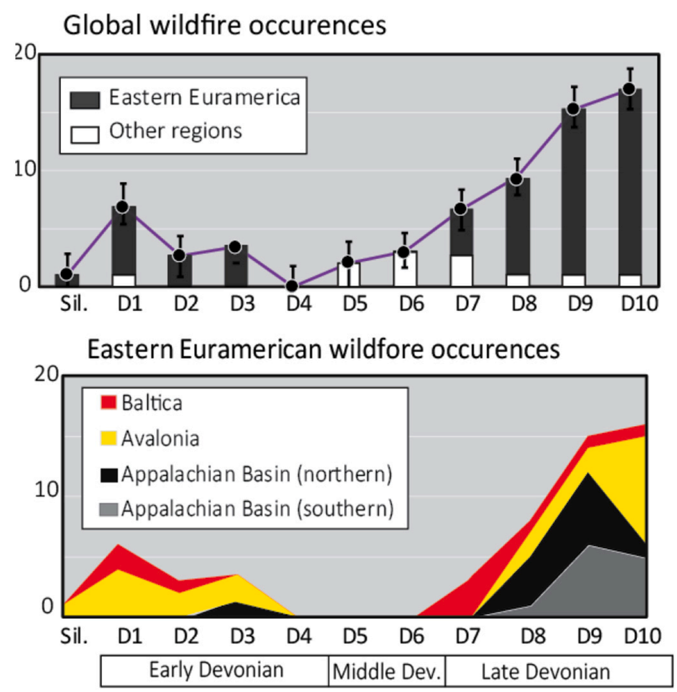

Fig. 2. Overview of the Silurian–Devonian wildfire record. Numbers with the letter 'D' on the x-axis represent the ten Devonian time bins. An associated statistical summary is available in Supplementary Table S1. Raw data of all wildfire occurrences are listed in Supplementary Table S2.

three study sites: a Hangenberg Black Shale Formation site in Poland (Devonian 10) (Marynowski and Filipiak, 2007; Marynowski et al., 2012), an outcrop with two successive members (Devonian 8 and 9) of the Chattanooga Shale Formation in Tennessee (Lu, 2020), and another Chattanooga Shale outcrop in Alabama (Lu et al., 2019). Of the 65 total occurrences, 64 entries came from clastic rock-dominant geologic units (i.e., shale, siltstone, or sandstone), and one was from an unspecified unit (and an uncertain rock type) in northwestern Germany (Wollenweber et al., 2006). Four reported sections (either outcrop or core) produced wildfire evidence from thin interbedded limestone layers. Of the occurrences in sedimentary rock, shale/mudrock showed the highest number ($n = 44$), and thirteen cases were reported from coal-bearing layers.

4.2. *Devonian wildfire occurrences in time and space*

A total of 65 wildfire occurrences included one in the Late Silurian, 12 in the Early Devonian, four in the Middle Devonian, and 48 in the Late Devonian (summaries in Fig. 2, Table 6, and Supplementary Table S1; raw data in Supplementary Table S2). The oldest known wildfire was from the upper Silurian Downton Castle Formation of Ludlow, U.K. (Glasspool et al., 2004). Around the globe, the very Early Devonian (Devonian 1 and 2; Lochkovian and Pragian) had seven and two wildfire occurrences, respectively, which are considerably higher than those of the late Early Devonian (Devonian 3 and 4: early and late Emsian) to the early Middle Devonian (Devonian 5: Eifelian). The Middle Devonian (Devonian 5 and 6: Eifelian and Givetian) to the early Late Devonian (Devonian 7: early Frasnian) displayed a relatively low value (lower than the average, 5.9 ± 6.0 occurrences, per unit). An overall increasing trend occurred throughout the Late Devonian (Fig. 2). Through all 10 Devonian time bins, significantly high values were found only in the early and late Famennian time bins (Devonian 9 and 10: $n = 15$ and 18 respectively) based on the upper 95% CI.

The increasing rates of wildfires across two consecutive time bins (Supplementary Fig. S2) showed an overall trend that is different from the count of the Devonian wildfire occurrences. Considerably high increasing rates appeared in a scattered manner throughout the Devonian although high wildfire frequencies appeared multiple times in

Table 6
Summary of Devonian wildfire occurrences through time and space. The Silurian record ($n = 1$) is not included. Raw data are available in Supplementary Table S2.

Paleogeographic regions	Devonian			Total	Mean + 95% CI
	Early	Middle	Late		
Appalachian Basin (southern)	0	0	12	12	1.2 ± 2.3
Appalachian Basin (northern)	1	0	11	12	1.3 ± 2.2
Avalonia	7	0	13	21	2.2 ± 2.8
Baltica	3	0	6	9	0.9 ± 1.1
Laurentia (north central)	0	2	1	3	0.3 ± 0.5
Laurentia (western)	0	0	2	2	0.3 ± 0.5
Siberia	0	1	0	1	0.1 ± 0.3
South China	0	0	0	0	NA
Tarim	0	1	0	1	0.1 ± 0.4
Africa	1	0	3	4	0.4 ± 0.7
Global (total)	12	4	48	64	6.3 ± 6.1
entire Euramerica (subtotal)	11	2	45	58	5.7 ± 6.1
eastern Euramerica (subtotal)	11	1	42	54	5.3 ± 6.0
outside Euramerica (subtotal)	1	23	3	3	0.9 ± 1.1

different paleogeographic provinces. The highest increasing rate (200%) appeared in the two Middle Devonian bins (the Devonian 5–6 Eifelian–Givetian transition), but this pattern did not appear in all paleogeographic areas. In contrast, relatively small increasing rates occurred globally in Devonian 8–9 and Devonian 9–10, but high values were found in the southern Appalachian Basin and Avalonia. In the Middle Devonian, wildfire evidence was distributed in this large paleogeographic area with spotted incidents/occurrences (outside of Euramerica). In the Late Devonian Frasnian–Famennian interval, reported wildfire remains were strictly concentrated in eastern Euramerica (the southern Appalachian Basin and Avalonia).

Of the 65 total occurrences, 59 were recorded from the Euramerica during the Devonian (Fig. 2; Table 6). Geographically, the Late Devonian wildfire record (Devonian 7–10) was highly concentrated in the eastern Euramerican region including the Acadian orogen along the Appalachian Basin and Avalonia landmass ($n = 45$ out of 48 in the entire Euramerica and 48 around the globe) (Figs. 3 and 4). In the global occurrences, the only two significantly high values (based on the upper 95% CI) that occurred in the two Famennian time bins (Devonian 9 and 10) were found only in Euramerica. While the highest occurrence ($n = 9$) was observed from Devonian 10 of the Avalonia region, wildfire occurrences remained constantly high in the Appalachian Basin through the Famennian (Devonian 9 and 10). Across the Frasnian–Famennian boundary, the distribution of wildfire evidence tended to expand from north to south along the Acadian landmass.

The topology and position of the major landmasses (listed in Table 4) changed through the Devonian (Supplementary Fig. S3). Based on the earliest and latest Devonian maps of Scotese (2014), the gap in the paleolatitudes occurred approximately or less than10 degrees exhibiting an overall northing trend for the paleowildfire distribution. This paleolatitudinal difference within the Late Devonian (i.e., Devonian 7 and Devonian 10) was about a few degrees), which had the highest count of paleowildfire evidence.

Paleolatitude-based occurrences of Silurian–Devonian wildfires showed that wildfire evidence was distributed in a restricted latitudinal range between 2° and 48° in both the paleo-northern and southern hemispheres (Fig. 3; Table 7; Supplementary Table S2, Table S3, and Fig. S4). The Shapiro-Wilk test indicated a normal distribution of wildfire occurrences relative to the paleolatitude ($P = 0.9061$). The mean value of the paleolatitudinal occurrences was 22.4° with the lower and upper 95% confidence interval as 10.89° and 33.85°, respectively. Significantly low latitudinal wildfires (i.e., below the lower 95% CI limit) were found in the Early Devonian (Devonian 1–4) ($n = 4$ out of 13) and the

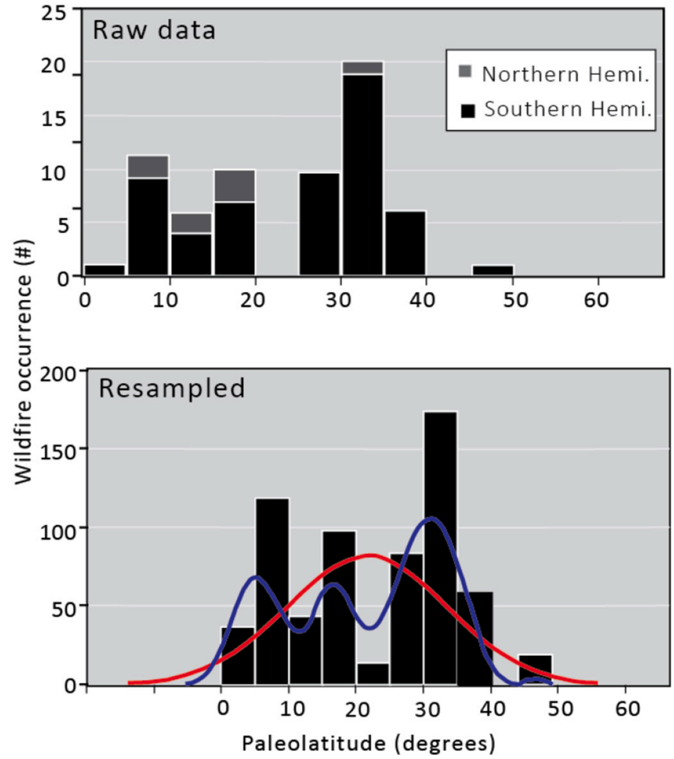

Fig. 3. Silurian–Devonian wildfire occurrences relative to paleolatitudes. *Top*: Raw data from the Northern and Southern hemispheres. X-axis indicates paleolatitudes in degrees with a combination of both hemispheres. *Bottom*: Bootstrap resampling replicated by 500 times with fit normal (red line) and Kernel density (blue line) curves. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Late Devonian (Devonian 7–10: $n = 11$ out of 48) (Supplementary Fig. S3). Based on the 5-degree intervals between 0° and 65° (i.e., 13 bins in total), the highest frequency occurred in the 30°–34° bin ($n = 20$). The second highest bin ranged in 5°–9°, which displayed 11 occurrences.

Based on the paleolatitude-based occurrences (Fig. 3; Table 7; Supplementary Fig. S4), Devonian wildfire evidence was recorded much more often from the paleo-Southern Hemisphere ($n = 58$) than in the paleo-Northern Hemisphere ($n = 7$). Wildfire occurrences from both the Devonian Northern and Southern Hemisphere data exhibited a normal distribution (Shapiro-Wilk test: $P = 0.9056$ and $P = 0.8117$). Paleowildfire evidence tended to be found at lower latitudes in the Devonian Northern Hemisphere (mean $= 8.0° \pm 3.8$) than in the Southern Hemisphere (mean $= 24.1° \pm 10.9$), yet statistically significant differences were not found (based on the 95% CI interval). The Devonian Northern Hemisphere occurrences came mostly from the northern Euramerica but also northern Baltica (northwestern Russian and Norway), north-central Laurentia (north-central Canada), and south of Siberia (i.e., possibly, in the Magnitogorsk Island Arc).

4.3. Devonian vascular plant diversity in Euramerica

Since the Devonian wildfire record showed a strong paleogeographic restriction in eastern Euramerica (Fig. 2; Supplementary Table S2), below we are presenting the Devonian vascular plant record only from the northern and southern Appalachian Basin, Avalonia, and Baltica. In the eastern Euramerican region across the 10 Devonian time-bins, 139 genera and 346 species of vascular plants (Tracheophytes) were recorded (an overview of the occurrences in Fig. 5 and Supplementary Table S4 and Table S5; raw data in Supplementary Table S6). Those eastern Euramerican vascular plants occurred in the current locations of 10 states of the eastern U.S., four provinces of eastern Canada, and 10

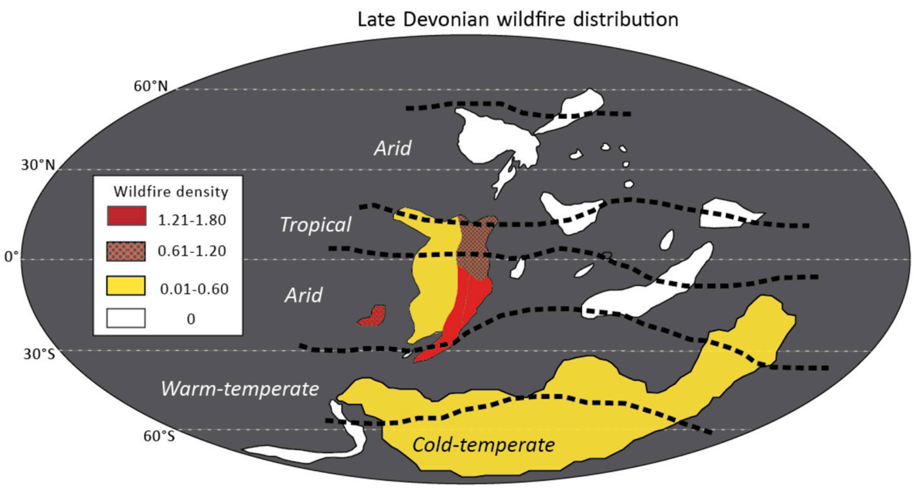

Fig. 4. Wildfire density distribution and paleoclimate during Late Devonian. The four ranks of wildfire density are established based on a wildfire count (log) and a relative surface area (log) (raw data available in Supplementary Fig. S4 and see Table S3 for further explanation). The map is redrawn based on the Famennian topology (about 370 mya) by Scotese (2014) and Golonka (2020). Names of paleogeographic regions are available in Fig. 1. Paleoclimate distribution is based on Hammond and Berry (2005).

Table 7
Descriptive statistic summary for paleolatitudinal occurrences (in degrees) of Silurian–Devonian wildfires.

	Global	Southern Hemisphere	Northern Hemisphere
Total (*n*)	65	58	7
Mean (in degrees)	22.4°	24.1°	8.0°
STDEV	11.5°	10.9°	3.8°
95% lower	10.89°	13.2°	4.2°
95% upper	33.85°	35.0°	11.8°
Minimum	2°	5°	2°
Maximum	48°	48°	15°
Shapiro-Wilk *P*	0.9061	0.9056	0.8117

western European countries. Through the 10 time bins of the Devonian, the largest species count was found in Devonian 10 (late Famennian) ($n = 72$). The same pattern was also found in the standing diversity (i.e., the data of all taxa including singleton species). Another notably high species count occurred in Devonian 6 (Givetian in the Middle Devonian). The species count tended to remain relatively low during the earlier Late Devonian (Devonian 7–9: early Frasnian to early Famennian) in eastern Euramerica.

The 346 Devonian vascular plant species consisted of six major representatives, including (i) basal vascular plants (stem and basal tracheophytes), (ii) stem lycopodiopsids, (iii) derived lycopodiopsids (including basal taxa within Lycopodiopsida), (iv) stem and basal lignophytes, (v) derived lignophytes, and (vi) the Pteridophytes–Monilophyta lineage (Table 3). Of the six main groups, the stem lycopodiopsid and the lignophyte groups exhibited the two highest counts (30 genera 62 species and 25 genera 98 species, respectively) (Fig. 5; Table 8; Supplementary Table S4). Their stratigraphic distributions, however, exhibited evident differences. The stem lycopodiopsid group occurred largely in the Early Devonian while the derived lignophytes were dominant in the Late Devonian (Fig. 6). The lycopodiopsid lineage including the stem and derived taxa were abundant during the Early (Devonian 1: Lochkovian) to the late Middle Devonian (Devonian 6: Givetian) but largely declined in Devonian 7 (early Frasnian) to Devonian 9 (early Famennian). This floral turnover shifting from the lycopodiopsids to lignophytes took place around the Givetian–early Frasnian boundary in eastern Euramerica.

A few other prominent taxonomic transitions during the vascular plant evolution were recognized in eastern Euramerica. During the Early Devonian, vascular plants were more abundant in the Avalonia region than in other paleogeographic areas, but the flora had started to disperse progressively to the Acadian region throughout the later Devonian (Fig. 5; Table 8). Since the oldest known tree taxon, *Eospermatopteris* (Cladoxylopsida), emerged on the land along the northern Appalachian Basin (the present location of New York) in the latest Givetian (Middle Devonian: Devonian 6) (Matten, 1974; Stein et al., 2007), the early forests composed of various trees and shrubs appeared to have expanded to a larger area in southeastern Euramerica.

Those trees and shrubs in eastern Euramerica mainly consisted of taxa of Lignophytes, especially archaeopterids, which had been dominant throughout the entire Late Devonian (Devonian 7 to Devonian 10). Cladoxylopsids constituted a relatively large proportion of early Frasnian forests (in Devonian 7), but they mostly disappeared in Devonian 8 to Devonian 9 across the Frasnian–Famennian (F—F) boundary and reappeared in Devonian 10 (late Famennian). Those basal vascular plants (paratracheophytes) had disappeared completely in the eastern Euramerica by the end of the Frasnian (Devonian 8) although their occurrences were scarce in the late Emsian (Devonian 4) to the late Frasnian (Devonian 8).

The Dominance Index of the basal tracheophytes showed the highest value (0.2619), indicating a relatively high evenness among the vascular plant taxa (Table 8). The second and third highest Dominance Index values were found in the stem lycopodiopsids (0.2390) and the lignophytes (0.2027).

Besides determining the overall trend of diversity derived from the species counts, we also compared the origination and extinction rates to identify temporally distinctive features (Fig. 7; Supplementary Table S5). The overall trend of the origination rates largely followed the temporal variation in the species count (Fig. 6), but a few differences were observed. In a total of 455 occurrences through the 10 time bins, including all singletons, the highest origination percentage was found in Devonian 5 (early Middle Devonian). The late Middle Devonian (Devonian 6: Givetian) also displayed a considerably high value, and another notably high origination percentage occurred in Devonian 2 (Pragian) (Fig. 6; Supplementary Table S4). The proportional origination (PO) values showed significantly high values (upper 95% CI: 2.362) in Devonian 6 (PO/myL = 2.82). The per-capita origination rate was significantly high in Devonian 2 and Devonian 6. While Devonian 2 and 6 exhibited considerably high origination rates, significantly high extinction values (Pe and Pemy) were found in the Givetian (Devonian 6).

5. Discussion

5.1. Analytical biases and sampling variations

Our global Silurian–Devonian wildfire data from published evidence reveal distinctive paleogeographic and stratigraphic distributions. Wildfire evidence is particularly abundant in eastern Euramerica during the Famennian (Devonian 9 and 10). Do the observed regional and time

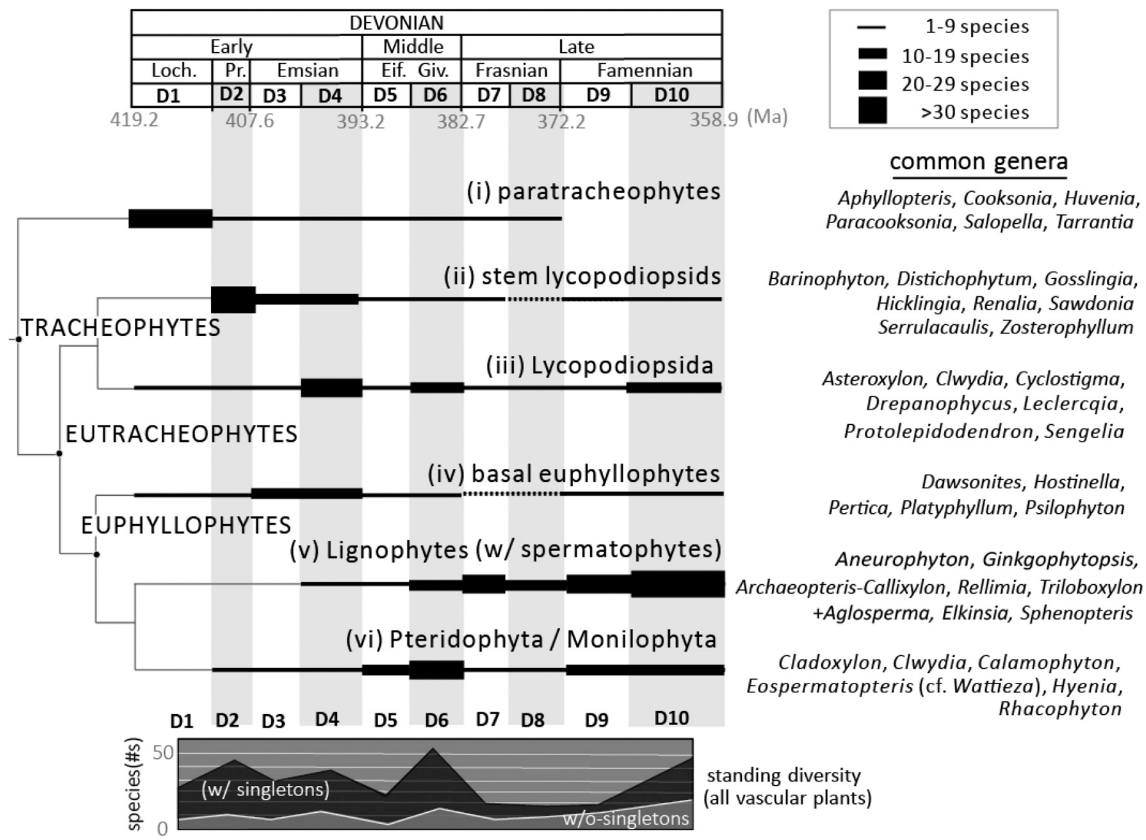

Fig. 5. Stratigraphic distribution of key vascular plant taxa in the eastern Euramerica during the Devonian. The cladogram is drawn based on Kenrick and Crane (1997), Gerrienne et al. (2016), and Crepet and Niklas (2018). Standing diversity of all vascular plants is calculated including (with) and excluding (w/o) singleton species separately. Explanations for each taxonomic group are available in Table 3.

Table 8
Summary of taxonomic counts and diversity index of vascular plants (Tracheophytes) from eastern Euramerica.

	w/	Singletons		w/o singletons	
	Genera	Species	Dominance Index	Genera	Species
All vascular plants	139	346	0.1104	39	93
pa: Paratracheophytes	20	36	0.2611	4	14
ly-1: stem lycopodiopsids	30	62	0.2390	8	12
ly-2: Lycopodiopsida	21	45	0.1413	9	18
eup: basal euphyllophytes	14	56	0.1768	5	14
lig: basal lignophytes (including spermatophytes)	25(11)	98(21)	0.2027	6(2)	35(11)
P-M: Pteridophyta/ Monilophyta	29	21	0.1847	7	10

Abbreviations for taxonomic groups and key taxa are listed in Table 3. Numbers with parentheses in the lig (lignophytes) row represent the species count of spermatophytes.

constraints represent the real pattern of the Devonian wildfire evolution? Or are these constraints merely a result of preservational and sampling biases? Moreover, paleogeographically, wildfire evidence is scattered or unknown in certain time bins for Siberia and North China in the Devonian Northern Hemisphere and South China, Tarim, and Gondwana in the Devonian Southern Hemisphere (Supplementary Table S2). Furthermore, the 10 Devonian time bin setting has a slightly different duration (Table 2). Considering these facts, do our data reflect a real paleowildfire evolution or mere sampling and preservational biases (e.g., due to an uneven number of researchers in regions or countries; irregular distribution of geologic units through the Devonian; specific ages or geologic units favored by researchers)?

The scattered nature of the record most likely represents a real diversification pattern of Devonian wildfires, rather than a result of some types of biases based on the following reasons. First, fossil charcoal evidence (including inertinites) is largely known from coal layers (e.g., the main data source of the three previous studies listed in Table 1), which have been well-studied and documented globally through the Paleozoic record. Second, although wildfire evidence is significantly scattered, extensive Lower and Middle Devonian sedimentary rock units exist globally (Tables 4 and 6). Third, our wildfire data paleogeographically concentrate in eastern Euramerica (Fig. 2). Theoretically, this spatial constraint pattern may result from sampling biases (e.g., geographic restriction of certain research groups and resources). A tremendous amount of coals and vascular plant fossils, however, are known globally from paleogeographic regions outside of eastern Euramerica, such as western Euramerica, Gondwana, Siberia, South China, and so on. As such, the most plausible explanation based on the currently available data is the very scattered or possibly absent nature of paleowildfire evidence in those paleogeographic areas.

To evaluate the magnitude of those types of potential biases on our dataset, an estimate of the relative abundance of samples (e.g., Devonian wildfires) in the paleontological record is essential (Raup, 1991). For this purpose, rarefaction has been used for various kinds of the paleontological and fossil records, including Devonian plants (Raymond and Metz, 1995; Alroy, 2010a, 2010b). Our rarefaction curve for Devonian wildfire occurrences across the count of geologic units (as a parameter of sampling effort) indicates that approximately 40–45 (or more) formations can provide a reasonable estimate (Fig. 8). The rarefaction curve also indicates that the 65 occurrences from the 37 formations in our

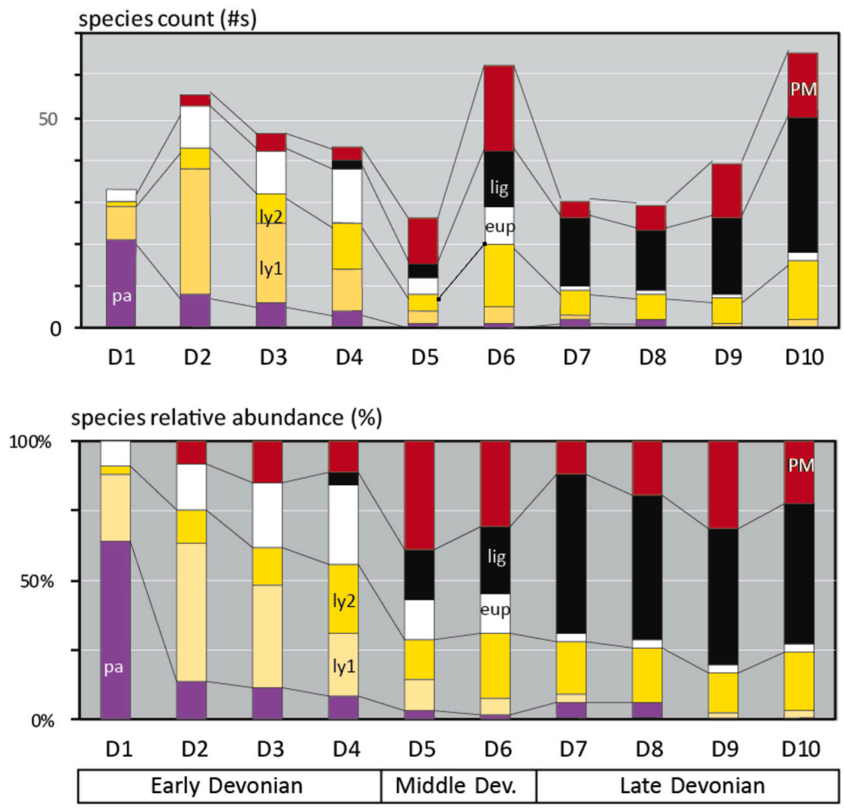

Fig. 6. Species count and relative taxonomic abundance of vascular plants in eastern Euramerica. A statistical summary is in Supplementary Table S4. The raw data used for the two graphs are available in Supplementary Table S6. Abbreviations for taxonomic groups: **pa**: paratracheophytes; **ly-1**: stem and basal lycopodiopsids; **ly-2**: derived lycopodiopsids; **eup**: basal euphyllophytes; **lig**: lignophytes (including spermatophytes); **P-M**: Pteridophyta/Monilophyta.

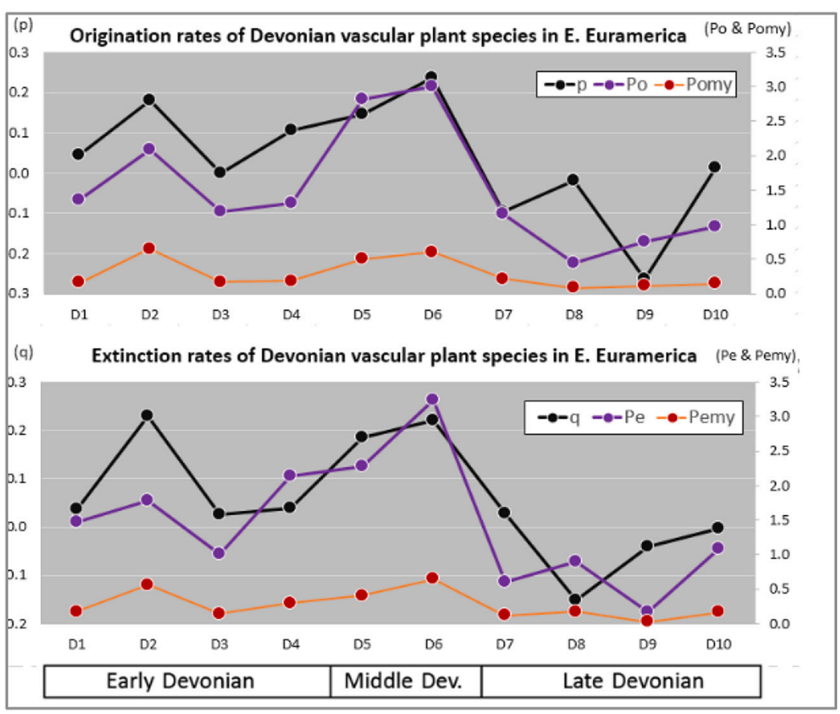

Fig. 7. Origination rates of Devonian vascular plants in the eastern Euramerica. **PO**: proportional origination (on the left y-axis); **PO/myL**: per million years; ***p***: per-capita origination rate (on the right y-axis). Additional data for the two graphs are available in Supplementary Table S5.

dataset can provide, at least, the minimum sample size for further investigation on the Devonian wildfire diversification.

To further assess potential problems of the relatively small sample size for data interpretations, the Bootstrap Resampling is a powerful method to reconstruct the overall data distribution by a mathematically estimated larger sample size. The bottom graph in Fig. 4 shows the resampled distribution of the Devonian wildfire occurrences along the paleolatitude on the X-axis based on the original data (the top graph in the figure). The actual and resampled data both exhibited a similar overall shape of a normal distribution, indicating that our data have a reasonable sample size to conduct additional analyses and further data interpretations.

We also examine the effect of the amount of previous studies regarding Devonian wildfires, that is, whether the number of studies is adequate to extract an overall diversity pattern. As a part of this inquiry, the relation between the publication record and the Devonian wildfire occurrences, as seen in the three previous studies (Table 1), is useful for identifying possible sampling biases. Since the first report of Devonian fire evidence in the 1960s (Ammosov, 1964), the number of publications remains considerably low over the following 30 years (i.e., until 1990) (Supplementary Fig. S1). A continuously increasing trend, however, has appeared since 2006. A noteworthy period is from 2011 until the present year (i.e., 2020), during which biomarker-based studies have been published more often than in the past. These recently accumulated data, we suggest, are robust enough to draw some conclusive interpretations on the global Devonian wildfire diversification as attempted by the three previous studies (Scott and Glasspool, 2006; Glasspool et al., 2015; Lenton et al., 2016).

Different sampling strategies for Devonian wildfires related to geological settings (e.g., various rock types, depositional environments,) can theoretically introduce a systematic error to the results from diversity studies of the fossil and paleoenvironmental records (Foote, 2000a; Peters, 2007; Alroy, 2010a, 2010b). To assess the effect of sampling strategies on our dataset, we compare the following factors: (i) preservation types (fossils vs. biomarkers), (ii) depositional setting (marine vs. terrestrial), (iii) sedimentary rock types (clastic vs. biochemical), and (iv) clastic rock types (shale vs. sandstone-siltstone). As a result of sampling variations (Table 5; Supplementary Table S2), more paleowildfire remains have been reported from marine sedimentary rocks, especially from shales, much more often than from fluvial units (sandstone and siltstone; but except for coal layers). At this point, no evident fact indicates a sampling bias or a different preservational setting for paleowildfire evidence in our dataset. Also, although our 10 time bin setting has different durations instead of an even time interval (e.g., 1, 5, or 10 million years) (Table 2), the gap in the range is considerably small (the mean and SD: 6.03 ± 1.47 million years). Also, information of descent stratigraphic ages is available for most paleowildfire data from those original fossil charcoal and biomarker studies and others (i.e., stratigraphy and sedimentology) (Supplementary Table S2).

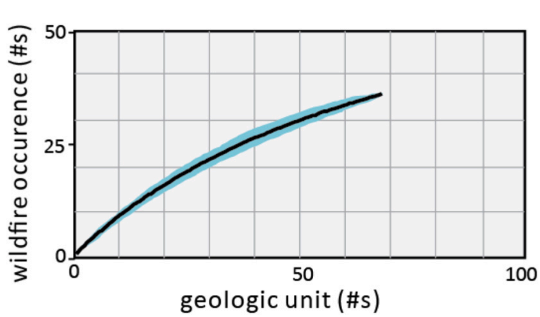

Fig. 8. Rarefaction curve of Devonian wildfire occurrences across a total number of geologic units (formations). A shaded area represents error bars. The graph is based on the data in Supplementary Table S2.

Our data on wildfire evidence types show that most previous studies largely relied on fossil charcoal evidence, but 17 out of 65 utilized solely biomarker for Devonian samples (Table 5; Supplementary Table S2). The 17 biomarker-based occurrences utilized the PAHs (pyrogenic *polycyclic aromatic hydrocarbons*), but only four of them combined both biomarker and fossil-based data (note: this counts a total of 69 entries for wildfire evidence due to the duplicates from both types). We suggest the biomarker approach certainly has advantages for gaining additional stratigraphic and paleogeographic data of Devonian and Silurian wildfires. Moreover, the biomarker technique allows investigating those units where visible charcoals are not preserved. The technique has been applied to not only the most investigated type of rocks, organic matter-rich shale, but biochemical sedimentary rocks (e.g., limestone) (Kaiho et al., 2013; Tulipani et al., 2015). A combination of fossil charcoal- and biomarker-based analyses of a successive section (e.g., outcrops, cores) can be powerful to determine a possible transformation of wildfire frequency and intensity in certain time and space, as demonstrated by a few studies (Marynowski and Filipiak, 2007; Lu et al., 2019; Lu, 2020).

In addition to the sampling strategy above, some plant tissue types likely serving as fuels can affect the quality and quantity of paleowildfire data. Fossil charcoals with woody tissues tend to have a better chance to be preserved (Nichols et al., 2000; Braadbaart et al., 2009; Scott and Damblon, 2010; Caromano and Cascon, 2014). Although various factors of a taphonomic process (e.g., original vegetation types, societal, combustion, settlement, and depositional filters, sedimentary and climate settings; Théry-Parisot et al., 2010) can theoretically affect the differential preservation of fossil charcoals, the quantity and quality of our Devonian data are too limited to conduct further study. To sum, we suggest that our Silurian–Devonian wildfire data provide sufficient information to extract overall diversity patterns and processes for further investigations to some degree.

5.2. The Middle Devonian charcoal gap revisited

Scott and Glasspool (2006) and Algeo and Ingall (2007) proposed the idea about the scarce nature of paleowildfire occurrences around the Middle Devonian based on the fossil charcoal evidence (inertinites). They independently coined the term, the 'charcoal gap' for this diversification trend that was suggested presumably to be associated with the relatively low atmospheric oxygen level. Their study, however, did not specify the exact stratigraphic range but likely applied to the entire Middle Devonian.

Our data (Fig. 2; Supplementary Table S1) indicate the charcoal gap does not only applies to the Middle Devonian (Devonian 5: Eifelian to Devonian 6: Givetian) but also extends to the late Emsian (Devonian 4) in the globe. No wildfire evidence has been reported from the Devonian 4 interval, and only one case has been known from Devonian 5 (i.e., the Eifelian Weatherall Formation of the Melville Island in Nunavut, Canada; Goodarzi and Gentzis, 2018). Three occurrences in Devonian 6 are recorded in northcentral Euramerica (the Melville Island in Nunavut-Northern Territory provinces, Canada), Devonian Siberia or the Magnitogorsk Island Arc (the Kuznetsk Basin in south-central Russia), and South China (Yunnan, southwestern China) (Supplementary Table S2) indicating the beginning of a possible wildfire dispersal trend in a wider geographic range.

Because of the existence of a large amount of sedimentary rocks and land plant fossils, we agree with Scott and Glasspool (2006) that the charcoal gap is most likely a real phenomenon rather than a distorted pattern created by sampling strategy or preservational conditions. Further exploration is certainly desirable for the time interval of interest (Devonian 5–7) in various regions and provinces in the future.

5.3. The primary fuel source of the 'Famennian Wildfire Explosion (FWE)'

Our data on the Devonian wildfire occurrences (Fig. 2) indicate that fossil charcoal and biomarker evidence from Famennian rocks (Devonian 9 and 10) is paleogeographically constrained in eastern Euramerica (Fig. 4). This high concentration in the paleogeographic region represents an extraordinarily paleoecological event in Paleozoic Earth's history. Here, we coin a term, 'the Famennian Wildfire Explosion' (FWE) for this possible unique paleoenvironmental phenomenon, which is characterized by a combination of (i) a rapidly increasing wildfire frequency after the Frasnian–Famennian boundary (in Devonian 9) and (ii) a constantly high occurrence of wildfires in the late Famennian (Devonian 10). The FWE revises the timing of the earliest wildfire spreading trend, 'the first tropical mires' in the Early Carboniferous (Scott and Glasspool, 2006), and pushes it further back to the early Famennian (as suggested by Algeo and Ingall, 2007). This revised idea is likely a result of the fact that, as mentioned above, their Silurian–Devonian data are based on much smaller sample size (i.e., nine references of fossil charcoal/inertinite occurrences) than ours (Table 1).

What taxonomic group(s) of woody plants (trees and shrubs) have possibly coevolved specifically with the Famennian Wildfire Explosion in eastern Euramerica? Most previous studies of Devonian wildfires suggested a coevolutionary scenario with the basal tree diversity or early forestation in a broad sense (e.g., Glasspool et al., 2015; Lenton et al., 2016), but specific taxonomic groups and data on their spatiotemporal distribution are not incorporated. For example, Rowe and Jones (2000) pointed out (all possible kinds of) woody plant taxa, such as lycopsids, cladoxylaleans, progymnosperms, and early seed plants (spermatophytes) are presumably the key fuel source, but a specific time(s) and paleogeographic region(s) nor statistical analyses are not provided. Walter Cressler III (Cressler, 2001; Cressler et al., 2010) proposed *Archaeopteris*, *Rhacophyton*, *cormose lycopsids*, *Gillespiea*, and various gymnosperms as the primary fuel sources based on the flora in the Catskill Formation of north-central Pennsylvania. This kind of taxa- and/or paleogeography-specified investigations for possible wildfire fuels, however, have not been largely applied to a larger region within and outside of eastern Euramerica due to limited data accessibility.

Our Devonian vascular plant diversity data (Figs. 5 and 6) indicate that the lignophyte-dominant forests are temporally and spatially corresponding to the FWE (Fig. 9). This type of forest, we propose here, is the best candidate for the main fuel source among the six common Late Devonian groups (Table 3). This idea is supported by the results of the Kendall's Tau correlation test ($P = 0.030$; correlation coefficient $\tau = 0.65$), which show that an increasing wildfire trend is largely concurrent with the diversification of lignophytes (Devonian 9: early Famennian) (Table 9; Supplementary Table S9). In contrast, a mix of all vascular plants does not strongly correlate with the wildfire distribution through the 10-time bins ($P = 0.255$), which further highlights the primary role of lignophyte forests as fuels. In addition, Devonian 6 (Late Middle Devonian: Givetian) shows a significantly high species count ($n = 63$) and origination rates (PO, PO/myL, and *P*; Fig. 7 and Supplementary Table S5) but does not display a high lignophyte abundance (relative to the six vascular groups (Fig. 6) and a high wildfire occurrence (Fig. 2). Our interpretation of the linkage between the FWE and lignophyte diversity agrees with a few previous studies (Cressler, 2001, 2006; Prestianni and Gerrienne, 2010; Shumilov, 2015).

Of numerous species of lignophytes, our distribution data (Fig. 5) display that taxa assigned as Aneurophytales, Archaeopteridales, and stem and basal gymnosperms (i.e., consisting of some taxa of the paraphyletic progymnosperms and basal spermatophytes) are the best candidates for the primary fuel of the FWE. In the Famennian (Devonian 9 and 10), 60 lignophyte species of the genera, including *Aglosperma*, *Aneurophyton*, *Archaeopteris*, *Ginkgophytopsis*, *Rellimia*, *Svalbardia*, and

Table 9
Kendall's Tau correlation test for possible controlling factors and Devonian wildfire occurrences.

	Fires	Plants (all)	Plant (lignophytes)	Rock units (#)	pO2%
Fires		0.469	0.027*	0.003*	0.234
Plant (all)	−0.18		0.779	0.925	0.929
Lignophytes	0.52	−0.07		0.032*	0.868
Rock units	0.69	0.02	0.50		0.505
pO2%	0.28	0.02	−0.04	0.16	

Plant diversity (species counts of all vascular plants and derived lignophytes) are compared for the wildfire sources. Rock volume (a count of formations) represents sampling variation. Atmospheric oxygen level indicates paleoclimate interaction. The numbers below the diagonal (left-bottom) are the τ values, and the numbers above the diagonal (right-top) are the *P*-values. An asterisk mark indicates a significant correlation ($P < 0.05$).

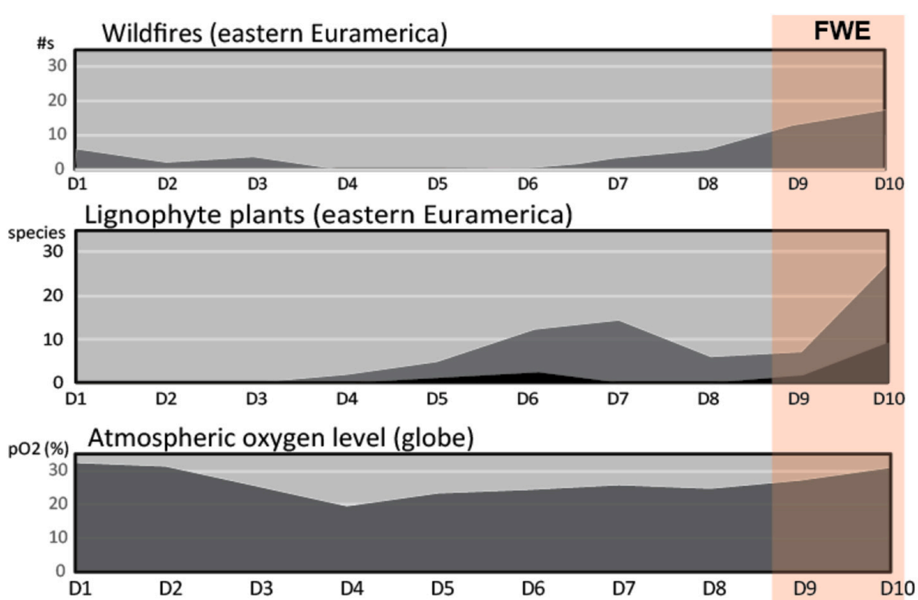

Fig. 9. Comparison of temporal trends for the Devonian wildfire occurrence, lignophyte diversity, and atmospheric oxygen level (pO_2) in eastern Euramerica. The black polygon in the graph of lignophyte plants represents spermatophytes. The pO_2 is adopted from Schachat et al. (2018). FWE refers to the Famennian Wildfire Explosion (explanation in the text). Raw data are available in Supplementary tables S2 (wildfire), S6 (lignophyte), and S7 (atmospheric oxygen).

Triloboxylon, are known across various states and provinces in the present location of eastern North America (i.e., eastern Euramerica) (Supplementary Table S6). The basal seed plant dispersal is prominent in the latest Famennian (Devonian 10) in eastern Euramerica (Supplementary Table S5 B), which may reflect an important role of dry environments in intensifying wildfire frequency (see further discussion on paleoclimate in the next section), as suggested as possible specific paleoclimate selectivity of some Devonian plant taxa for the primary habitat (Wan et al., 2019).

It is worth noting that abundant fossils of Late Devonian woody plants have been also found from outside of Euramerica. For example, in South China, lycopodiopsids are suggested to be the most dominant component of forests (Xiong et al., 2013; Xue et al., 2018). Numerous well-preserved lignophyte fossils are reported from Siberia (Korzhnev, 2014) and parts of Gondwana (Anderson et al., 1995; Meyer-Berthaud et al., 1997; Gerrienne et al., 2010). These facts indicate that the forestation progresses globally rather than only in eastern Euramerica. The series of circumstantial evidence leads us to the interpretation that the paleogeographically concentrated distribution of wildfire evidence in eastern Euramerica reflects the real pattern of the paleowildfire diversification, instead of vague sampling and preservational biases.

Furthermore, most Famennian lignophytes commonly exhibit flammable characteristics, such as a gigantic overall size, wood tissues, and newly evolved leaf traits (e.g., overall sphenopterid and whorled shapes; leaf abscission; Chaloner and Sheerin, 1979). Larger trees generally possess a higher number of leaves and branches, which can be the biggest fuel source in modern wildfires (Dodge, 1972; Moreno-Sánchez, 2004; Campbell et al., 2012; Keane, 2015; Belcher, 2016). The increasing size of Late Devonian vascular plants was suggested to be more evident in the Laurasia (including eastern Euramerica) than other paleogeographic regions (Raymond, 1987; Xue et al., 2015). During the Famennian, large whorled or sphenopterid-shaped leaves first appeared in various lineages of vascular plants (Chaloner and Sheerin, 1979; Hao and Xue, 2013). The appearance of those morphological features in the vascular plant evolution can play an important role in the FWE. To further confirm this hypothetical scenario, more accurate data on the timing of synapomorphies in each tracheophyte clade will be needed.

5.4. Implications of the Famennian Wildfire Explosion for paleoclimate

Historically global wildfire episodes, such as the FWE (Famennian Wildfire Explosion) proposed here, must have relevance to a certain kind (s) of paleoclimate conditions. Among numerous climate factors, we test and compare the following three conditions as possible candidates – the atmospheric oxygen level, paleolatitudinal gradient, and paleohumidity. The pO_2 has been suggested to be one of the main controlling factors for the wildfire frequency in both modern and geologic settings (Uhl and Kerp, 2003; Scott and Glasspool, 2006; Glasspool and Scott, 2010, 2013; Uhl et al., 2008; Brown et al., 2012; Abu Hamad et al., 2012; Rimmer et al., 2015; Huang and Rein, 2016). Some studies demonstrate rapidly increasing pO_2 values throughout the second half of the Late Devonian (Robinson, 1991; Berner et al., 2003; Glasspool et al., 2015; Schachat et al., 2018). Following this atmospheric oxygen evolutionary trend, numerous studies integrated a hypothetical explanation for this continuously increasing pO_2 trend as the key driver for the rise of the Devonian wildfire diversification (e.g., Chaloner, 1989; Cressler, 2001; Scott and Glasspool, 2006; Glasspool and Scott, 2013; Glasspool et al., 2015; Rimmer et al., 2015; Lenton et al., 2016; Liu et al., 2020; Scott, 2020). However, no studies have yet incorporated statistical analyses (e.g., correlation) to evaluate the relative timings of the two parameters, and the actual pO_2 data over the entire Late Devonian (i.e., Devonian 7–10) were not presented in those studies (e.g., Fig. 1 of Glasspool and Scott 2010).

Our Devonian wildfire data provide the first opportunity to determine whether the Devonian wildfire and pO_2 level covary at a finer temporal resolution (i.e., the 10-time bin setting). Based on the Devonian data extracted from Schachat et al. (2018), the pO_2 level is significantly higher in the two Famennian time bins (based on the 95% CIs of the entire Devonian: 26.60% ± 4.02) and peaks in Devonian 10 (late Famennian: ca. 31.15%) (Supplementary Table S7). As seen in Fig. 9, this sharply increasing trend starts around the transition of the early and late Frasnian (Devonian 7 and 8), but a fluctuating pattern also appears through the late Emsian (Devonian 4) to the early Frasnian (Devonian 7). Moreover, a gradually decreasing trend is observed at Devonian 7, and the most evident divergence occurs during the Frasnian. These fluctuating patterns of pO_2 in the pre-Famennian time do not match well with the occurrence of the wildfire evidence. While a continuous increase in the wildfire evidence count is found in Devonian 7 and 8, the pO_2 level shows a contradictory decreasing trend. Moreover, although the pO_2 level gradually increases through the late Emsian (Devonian 4) to the early Frasnian (Devonian 7), the wildfire evidence is scattered or absent in the Middle Devonian.

Since the fuel type is another essential factor for the wildfire frequency, we quantify the relative timings and compare the correlation of the lignophyte diversity peak and the rapidly increasing oxygen level through the Devonian. Results of the Principal Component Analysis (PCA) show that the first two principal components exhibit 92.0% of the total variance (Fig. 10, Supplementary Table S9 and Fig. S5). The PCA data further show that the lignophyte vector shows strongly positive correlations (PCA correlation > |0.5|) with the first two primary components (PC 1 and PC 2). On the other hand, the wildfire vector is poorly aligned to the pO_2 likely due to the increasing pO_2 trend in Devonian 4 (late Emsian) (Fig. 9). Another weak correlation with paleowildfire is found with another vector of all vascular plants, which can be due to relatively high species counts of all vascular plants in Devonian 2 (late Early Devonian: Pragian) and Devonian 6 (late Middle Devonian) (Fig. 6). These data indicate a unique paleoecological setting that may control the FWE in the late Famennian (Devonian 10), which may display a stronger linkage with the lignophyte diversity than the pO_2 level throughout the Devonian (Table 9).

Besides the lignophyte forests as the major fuel source, paleoclimate conditions associated with the latitudinal gradient can also play an important role for the FWE. The largest wildfire frequency is reported at about 50° of the Devonian Northern Hemisphere in the modern environmental setting (Giglio et al., 2006; Flannigan et al., 2009). This latitudinal zone, based on the Koppen-Geiger climate classification, is largely assigned to the semi-arid and warm temperate climate zones (Peel et al., 2007). In the longitudinal range, these types of climate largely host dense forestry vegetation in the modern environment (Keith et al., 2009). In contrast, the Devonian wildfires are largely distributed

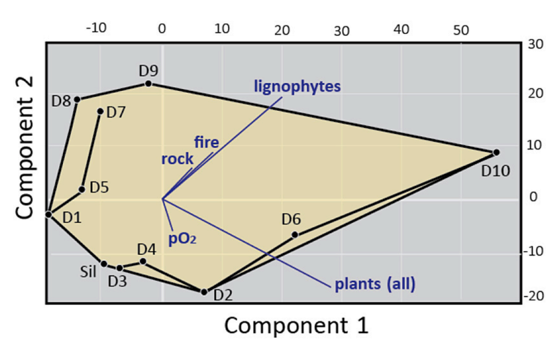

Fig. 10. Principle Component Analysis (PCA) biplot for comparisons of possible controlling factors among the Silurian and 10 Devonian time bins (light yellow polygon). The wildfire occurrence (fire) shows a more positively correlated relation with the lignophyte species count (lignophytes) and rock unit count (rock) than with the pO_2 level and all vascular plants (plants (all)) based on the directions of blue vectors. Each PCA value, eigenvalue, and variance (%) are shown in Supplementary Table S9 and Fig. S5. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

in a lower paleolatitudinal zone (the average of 22.0° ± 11.3 in the Devonian Southern Hemisphere: Figs. 3 and 4; Supplementary Fig. S3 and Table S3). This paleogeographic area largely comprising the eastern Euramerica is suggested to be under an arid climate in the Late Devonian (Fig. 4) (Hammond and Berry, 2005; Kaiho et al., 2013; Shen et al., 2019). By comparison, fireless environments and climates are identified in South China (i.e., very wet, low latitudinal climate), Siberia, and southern Gondwana (i.e., cold, relatively wet high latitudinal climate) during the Late Devonian based on the global paleo-humidity model from Le Hir et al. (2011) (Fig. 4).

Relatively high wildfire occurrences constrained by an arid climate in a certain paleolatitudinal range can be a unique feature for the FWE. This feature is in contrast with the high fire frequency in a more humid area, which is known for Early Carboniferous tropical forests (Falcon-Lang, 2000; Scott and Glasspool, 2006). One of the possible explanations for extensive Famennian wildfires in low-latitude areas is due to the spatial evolution of lignophyte-dominant early forests on eastern Euramerica. The largely synchronizing pattern (besides others) of the Devonian wildfire diversity (Fig. 2) and the early lignophyte evolution (Fig. 5) may indicate that the dispersal of those early forests can be expanded further to drier inland areas of the Acadian Orogen and Avalonia for the first time in plant history as demonstrated by a paleoclimate model (Le Hir et al., 2011). To further test this hypothetical scenario, locality-based paleowildfire analysis, rather than state, province, and country-based analyses as presented in this study, will be necessary.

6. Conclusions

Studies of the Devonian wildfires have been gradually accumulating in the last few decades. Fossil charcoal is the commonly used type of evidence for identifying Devonian wildfires, but biomarker-based evidence (PAHs) has the potential to expand the quantity of data in time and space from various kinds of rocks (including some non-coal and non-plant fossil-bearing strata). The currently available global data are statistically robust enough to extract an overall pattern of the Devonian wildfire diversification. Our data show scattered wildfire remains from the late Early to the end-Middle Devonian (representing a revised duration of the charcoal gap trend), but the occurrences continuously increase throughout the Late Devonian. During the Late Devonian, a significantly high frequency based on the occurrence count is found from Famennian strata, which refers to the Famennian Wildfire Explosion (FWE). The FWE is likely driven by the diversity of lignophyte-dominant forests (exhibiting shrub and large tree taxa with abundant wood tissues and developed flammable branches and leaves) that are primarily constrained in eastern Euramerica.

Our data on the Devonian wildfires and vascular plant diversity provide some insights on paleoclimate. The paleolongitudinal distribution of the paleowildfire evidence exhibits the highest concentration at about 22.0° ± 11.3 in the Devonian Southern Hemisphere. This find suggests that paleowildfire frequency may be related to arid to semi-arid warm temperate climate. In contrast to some previous studies, our data do not strongly support the idea that the pO_2 level drives the rise in wildfire through the Late Devonian. Instead, the FWE is likely a phenomenon resulting from the first adaptation and dispersal of early vascular plants in relatively arid inland environments in plant history. Ultimately, our study demonstrates that the Paleozoic wildfire data have the potential to be utilized as paleoecological and paleoclimate indicators (e.g., vegetation types, aridity, atmospheric oxygen level). To gain better understandings of paleowildfire diversification patterns and processes with a higher resolution, a larger quantity and better quality of evidence will be direly needed.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2021.110321.

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