Sampling biases and Paleozoic sporomorphs diversity dynamics in Western Gondwana strata

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ABSTRACT

A dataset consisting of presence-absence data of 137 pollen and spore genera was elaborated with published sources from Pennsylvanian and Permian Atlantic (Paraná, Parnaíba, Amazonas, and Claromecó) and Pacific (Paganzo, Tarija, and Madre de Dios) basins of South America. The richness and origination, extinction, and sampling rates of sporomorphs were analyzed in order to address the effect of sampling biases over diversity estimations. Richness and sampling were estimated using the recently developed True Richness estimated using a Poisson Sampling (TRiPS) model. Origination, extinction, and sampling rates were estimated with Inverse Survivorship Models. The TRiPS analysis showed changes in richness during the studied interval. The highest richness was observed for the Cisuralian, and the lowest richness was recovered for the Pennsylvanian and Guadalupian. The best supported Inverse Survivorship Model revealed that the highest origination values occurred between the Gzhelian and Asselian, whereas the highest observed extinction rate occurred between the Kungurian and the Roadian. In particular, pollen grains showed higher net diversification than spores, while spores showed higher turnover than pollen grains. Also, an alternation in richness dominance was observed at the beginning of the Permian, with pollen grains showing higher richness after the Artinskian. Changes in total sporomorphs diversity, as well as differences between spores and pollen grains, may be related to changing climatic conditions in Western Gondwana during the late Paleozoic (from icehouse to greenhouse conditions) that could impact differently over plant communities. Although the fossil palynomorph record has been widely used as a biostratigraphic tool, our results highlight its importance and usefulness for the study of plant communities and their evolution in the past.

1. Introduction

Changes in palynofloras from several basins in South America (Beri et al., 2015, 2018 and references therein) reflect the effect of climate on vegetation during the late Paleozoic transition from a glacial state to the full greenhouse conditions recorded across Gondwana (e.g., Gastaldo et al., 1996; Rees et al., 1999; Montañez and Poulsen, 2013). The relationship between floral diversity and climate is well-known, with floral diversity in equatorial-tropical climatic zones being higher than in temperate or cold climatic zones (e.g., Scheiner and Rey-Benayas, 1994; McGlone, 1996; Iannuzzi and Rösler, 2000). There are numerous palynological studies of glacial and post-glacial sequences in Western Gondwana that support palynostratigraphic proposals erected

from distinct approaches (e.g., Playford and Dino, 2000a, 2000b; Césari and Gutiérrez, 2001; di Pasquo, 2003; Souza and Marques-Toigo, 2003, 2005; Souza, 2006; Gutiérrez et al., 2018; Beri et al., 2011; Gutiérrez and Balarino, 2019). Recently, the global diversity patterns of vascular plants have been examined in several studies (e.g., Jaramillo et al., 2006; Cascales-Miñana et al., 2010; Cleal and Cascales-Miñana, 2014; Cascales-Miñana et al., 2018). However, few studies have focused on the use of palynology as a tool for the study of past plant diversity on a continental scale.

There are numerous biases when using pollen richness as an indicator of floristic richness (Birks and Line, 1992), such as variations in pollen and spore production and dispersion. In particular, several authors have studied the relationship between plant diversity and pollen
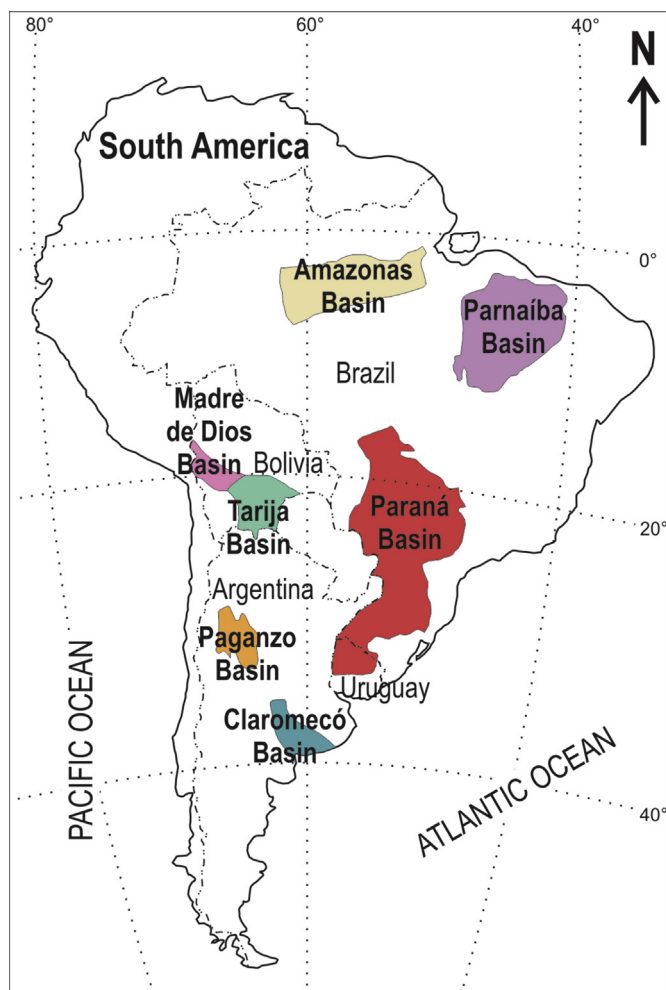
Fig. 1. Location of the Amazonas, Parnaíba, Paraná, Claromecó, Paganzo, Tarija, and Madre de Dios basins.

data (e.g., Odgaard, 1999; Weng et al., 2006). Moreover, the extent to which the fossil record reflects biological diversity has long been debated, and different ways of incorporating or minimizing the effects of biases have been proposed (e.g., Raup, 1972; Foote, 2000, 2001; Benton et al., 2000, 2011; Alroy, 2014, 2015; Cascales-Miñana et al., 2013).

This paper aims to analyze the richness, as well as the origination, extinction, and sampling rates of sporomorphs in Pennsylvanian to Lopingian strata in order to address the effect of sampling biases over diversity estimations and explore different hypotheses regarding diversity dynamics. The palynological contents extracted from the South American Paraná, Parnaíba, Amazonas, and Claromecó basins (denominated as Atlantic basins) and the Paganzo, Tarija, and Madre de Dios basins (denominated as Pacific basins; Fig. 1) are analyzed using the True Richness estimated using a Poisson Sampling (TRiPS) model (Starrfelt and Liow, 2016) and Inverse Survivorship Models (Foote, 2001; 2003a, 2003b, 2005).

2. Geological setting

2.1. Atlantic (intracratonic) basins

The intracratonic basins of Paraná, Amazonas, and Parnaíba document a significant sedimentary-magmatic record distributed through extensive areas. According to Milani and Zalán (1999), the upper Paleozoic filling of these basins corresponds to siliciclastic sedimentary sections, except for an evaporite-carbonate sequence of the Amazonas basin. This basin covers ~500,000 km^2 and lies completely under the

Amazon forest, so most of their geological and paleontological data come from subsurface sections. Relative age data are mainly provided from conodonts, foraminifers, and spore-pollen associations (e.g., Lemos, 1992a, 1992b; Altiner and Savini, 1995; Playford and Dino, 2000a, 2000b; Scomazzon, 2004; Nascimento et al., 2005).

The Parnaíba Basin is located in the western portion of the northeastern region of Brazil and occupies an area of 600,000 km^2 (Fig. 1). The Pennsylvanian-Triassic section of this basin is represented by the Balsas Group, which is composed by the Piauí (late Pennsylvanian), Pedra de Fogo (Permian), Motuca, and Sambaíba formations (the last two of uncertain Permian/Triassic age; Vaz et al., 2007). Among the three basins mentioned above, the Parnaíba Basin is the least known in a geological and paleontological context. The relative ages of the units are based on palynomorphs derived from a few outcrops of specific stratigraphic horizons and subsurface studies (Dino and Playford, 2002; Iannuzzi et al., 2003; Melo and Loboziak, 2003; Souza et al., 2010a).

The Paraná Basin covers an area of over 1,000,000 km^2 in the central-south portion of Brazil, also reaching the neighboring countries of Paraguay, Argentina, and Uruguay (ca. 400,000 km^2), where it is named as Chaco, Chacoparaná, or Northern Basin, respectively (Fig. 1). The Upper Paleozoic deposits of this basin correspond to the Gondwana I Supersequence of Milani (1997), which includes a heterogeneous and complex package produced by drastic paleoenvironmental changes from the Gondwana glacial epochs (Pennsylvanian) to the dry and arid Triassic times (Milani and Zalán, 1999). This Supersequence is represented in ascending stratigraphic order by the Tubarão (Itararé Subgroup, Rio Bonito, Palermo formations) and the Passa Dois (Irati, Serra Alta, Teresina, and Rio do Rasto formations) groups, which are covered by eolian and fluvio-eolian deposits of late Permian or early Triassic age (Pirambóia and Sanga do Cabral formations), as summarized by Milani et al. (2007). The relative ages for these deposits are mainly derived from spore-pollen associations, and plant remains (e.g., Mori and Souza, 2012; Iannuzzi, 2013; Bernardes-de-Oliveira et al., 2016; di Pasquo et al., 2017a; and references therein), with some horizons bearing certain vertebrates and invertebrates (see Holz et al., 2010).

The south-eastern portion of the Paraná Basin extends into northern Uruguay, occupying an area of approximately 90,000 km^2 (de Santa Ana et al., 2006). Palaeozoic outcrops are distributed throughout an area of 24,000 km^2 in the Cerro Largo, Tacuarembó, Rivera, and Durazno departments, while the rest of the sequence is covered by Lower Cretaceous extrusive rocks and younger sedimentary rocks (Andreis et al., 1996). According to de Santa Ana et al. (2006), the beginning of the Neopalaeozoic sedimentation is characterized by extensive glacial, glacial-marine, or glacial-influenced sedimentary records. These Permo-Carboniferous sedimentary successions are represented, in ascending stratigraphic order, by the San Gregorio, Cerro Pelado, Tres Islas, Frayle Muerto, Mangrullo, Yaguarí, and Buena Vista formations (de Santa Ana et al., 2006). Palynological datings of these Permian units are based on subsurface studies (e.g., Beri et al., 2011, and references therein).

The Neopaleozoic succession in the Claromecó-Sauce Grande-Colorado Basin (50.000 km^2) corresponds to the Pillahuincó Group (Sauce Grande, Piedra Azul, Bonete, and Tunas formations) and their relative ages based on palynological studies indicate a late Pennsylvanian–Permian age (Archangelsky et al., 1996; di Pasquo et al., 2008; Balarino, 2014). Invertebrates and plant fossils that support a Cisuralian age are also present mostly in Piedra Azul and Bonete (see Azcuy et al., 2007, Fig. 1).

In recent years, new radiometric ages of individual zircons were obtained from tonsteins and subaerial volcanic ash deposits within the Pennsylvanian-Permian sedimentary succession of the Paraná Basin in Brazil and Uruguay. Although many discrepant results were observed, sometimes even for the same locality, there is a tendency that shows an improvement of the used techniques and the subsequent adjustment of the results. Many of these levels were reanalyzed by Griffis et al. (2018), who considered the glacial deposits as entirely Carboniferous,

with the terminal deglaciation in the west-central Gondwana occurring near the Permian-Carboniferous boundary. These interpretations are in accordance with the general scheme proposed by Rocha-Campos et al. (2019), which is also based on radiometric data from various units of this sedimentary succession. The biostratigraphic data are continually being evaluated, and modifications should be proposed in the near future, such as the first appearance of the genus *Vittatina* and allied forms in older levels within the late Pennsylvanian. Regarding the Amazonas and Parnaíba basins, no radiometric ages are currently available. Finally, for the Claromecó-Sauce Grande-Colorado Basin, Arzadún et al. (2018) obtained absolute ages from subsurface and surface ashes of the Tunas Formation that indicate an early Cisuralian age.

2.2. Pacific basins

The upper Paleozoic strata of the Tarija Basin extend from northern Argentina (~23° South latitude), including the Subandean Range and part of the Cordillera Oriental, the subsurface of the Chaco-Salteña plain in Argentina and extensions in southern Bolivia up to the latitude of Santa Cruz de la Sierra (17°–18° South latitude), and the northwestern portion of Paraguay (Fig. 1). An inflection of the Andes mountains occurs at that latitude, and the Madre de Dios Basin is developed, embracing northern Bolivia and southern Peru (Azcuy and di Pasquo, 2000; Suárez Soruco, 2000). The clastic deposits of the Macharetí, Mandiyutí, and Cuevo and the clastic and calcareous deposits of the Titicaca groups characterize the Pennsylvanian Ice Age and a climatic amelioration during the Permian. They are palynologically productive and allowed correlations with other Gondwanan basins (e.g., Azcuy and di Pasquo, 2000; Azcuy et al., 2002; di Pasquo, 2003, 2007, 2009a, 2009b; di Pasquo and Grader, 2012; di Pasquo et al., 2015, 2017b, 2019; and references therein).

The Carboniferous–Permian sedimentary sequences of the Paganzo Basin in Argentina are related to glacial and post-glacial environments and correspond to the transgressive/regressive cycles that comprise the Paganzo Group (Fig. 1). Numerous palynological studies supported biostratigraphic schemes, and paleoenvironmental and paleoclimatic inferences have been proposed (e.g., Archangelsky, et al., 1996; Azcuy et al., 2000, 2007; Césari et al., 2011; Césari and Chiesa, 2017; Gutiérrez et al., 2017, 2018; Limarino et al., 2014; Valdez et al., 2017a, 2017b; and references therein). The palynological zones described for the pacific basins in Argentina are among the best known in South America. The distribution of palynomorphs (spores-pollen and acritarchs) recorded in the different lithostratigraphic units of these basins allowed the recognition of four Palynological Assemblage Zones, comprising ages from the Bashkirian to the Roadian, as well as the Changhsingian (Gutiérrez et al., 2018). Furthermore, the ages of these units have been calibrated with radiometric datings in the recent years (Césari, 2007; Césari et al., 2011; Gulbranson et al., 2010; Rocha-Campos et al., 2011; Valdez et al., 2017a, 2017b; Vazquez and Césari, 2017).

3. Material and methods

A dataset consisting of presence-absence data of 137 pollen and spore genera of Pennsylvanian–Lopingian age from Atlantic and Pacific basins was elaborated from published sources (Supplementary Table 1). The database was assembled with data from palynoassemblages with precise lithostratigraphic and age information. Although the authors' original chronostratigraphic proposals were used for the age assignment of taxa occurrences, corrections were made according to the most recent schemes (Rocha-Campos et al., 2019). For the geochronologic assignment of taxa occurrences, the most recent international chronostratigraphic chart (Cohen et al., 2019) was used.

The genera used in this study include all relevant species, considering synonyms provided in publications and avoiding superfluous species as much as possible (e.g., undetermined species of a genus were

not included unless it was corroborated with a picture and/or a description).

Selected works of the Paraná Basin from Brazil (Ybert, 1975; Cazzulo-Klepzig et al., 1980; Dias-Fabrício, 1981; Marques-Toigo et al., 1982, 1984; Picarelli et al., 1987; Souza et al., 1997, 2003, 2010a, Souza et al., 2010b; di Pasquo et al., 2003a, 2003b, 2017b; Iannuzzi et al., 2006; Premator et al., 2006; Souza, 2006; Neregato et al., 2008; Mori and Souza, 2010, 2012; Boardman et al., 2012a, Boardman et al., 2012b) and Uruguay (Mautino et al., 1998a, 1998b, 1998c; Beri and Pecoits, 2001; Gutiérrez et al., 2010; Beri et al., 2011, 2013a) are included into the database together with data from the Parnaíba (Dino and Playford, 2002; Dino et al., 2002), Amazonas (Playford and Dino, 2000a, 2000b), and Claromecó (di Pasquo et al., 2008) basins.

For the Tarija Basin, di Pasquo and Azcuy (1997, 1999), di Pasquo et al. (2001), di Pasquo et al., 2017a, di Pasquo (2002, 2003, 2009a), del Papa and di Pasquo (2007), di Pasquo and Noetinger (2008), di Pascuo and Vergel (2008), and Aráoz et al. (2016) were considered. Data from Azcuy et al. (2002), di Pasquo (2009b), di Pasquo and Grader (2012), and di Pasquo et al. (2015) were utilized for the Madre de Dios Basin. di Pascuo et al., (2010) and Valdez et al. (2017a) were used for the Paganzo Basin.

Sporomorphs richness and sampling were estimated using the recently developed TRiPS method (Starrfelt and Liow, 2016). This method uses the number of times that species are observed in the fossil record in order to simultaneously estimate richness and sampling bias in each time interval. In particular, TRiPS assumes that, in a specific time interval, taxa observed multiple times have a relatively high probability of fossilization and modern-day discovery. The method uses information across taxa that are likely to have similar potential for fossilization and modern-day rates of discovery to estimate the number of species that may be missing and, therefore, the true number of taxa that might have existed. This approach has the advantage of estimating true richness, in contrast to the relative richness estimation obtained using other approaches, while simultaneously estimating sampling bias. However, this richness estimation could suffer from an underestimation of richness, especially with low and unequal sampling coverage across time (Close et al., 2018).

We estimated overall sporomorphs richness as well as spores and pollen grains separately in order to explore differences between both groups. Furthermore, origination, extinction, and sampling rates were estimated with Inverse Survivorship Models (Foote, 2001, 2003a; 2003b, 2005) implemented in the R package paleoTree (Bapst, 2012) using the functions "make_inverseSurv" and "constrainParPaleo." This approach allows the implementation of different models accounting for different rates of each parameter in each time interval. Likewise, different rates can be considered for different groups in the data. These more complex models can be evaluated in contrast to simpler models, where constant rates in time or equal rates across groups are assumed. In particular, in order to account for sampling biases in the data, we tested whether modeling different sampling rates across time significantly improved model fit and thus could affect origination and extinction estimations.

Moreover, we tested for the existence of different origination and extinction rates between spores and pollen grains. In total, five models, considering possible combinations of constraints, were fitted to the data (Table 1). The first model assumed constant origination, extinction, and sampling rates and was considered as a null hypothesis, while other models assumed variable or constant rates in some parameters. In this regard, the tested alternative hypotheses assumed variable origination and extinction rates or variable sampling rates. In particular, the last model assumed variable origination and extinction rates with a constant sampling rate and considered spores and pollen grains separately in order to test different dynamics between these taxonomic groups. In all cases, the probability of sampling a taxon before the first interval or after the last interval was set to 0.5 in order to reduce potential extreme values in the first and last intervals. However, parameter values for

Table 1
Model fits for the Inverse Survivorship analysis.

Model	N° of parameters	log likelihood	AIC	AIC weight
Constant origination, extinction and sampling rates	3	−634	1274	< 0.001
Constant origination and extinction rates and variable sampling rate	14	−614	1256	< 0.001
Variable origination, extinction and sampling rates	36	−458	988	< 0.001
Variable origination and extinction rates and constant sampling rate	25	−458	966	0.167
Variable origination and extinction rates and constant sampling rate considering pollen and spores independently	50	−431.4	962.8	0.832

these intervals should be considered with caution. All analyses were carried out using range-through data, assuming that taxa occur at all time intervals from the base of the interval they appear in the record in our database up to the end of the last interval they occur in. Considering the scarce data available for the Lopingian, this time interval was not subdivided in ages. Finally, the models were evaluated through their Akaike's Information Criterion (AIC) values, and model support was summarized with AIC weights.

4. Results

The TRiPS analysis showed some changes in genus richness through the studied interval. The highest richness was observed in the Cisuralian, whereas the lowest richness was recovered for the Pennsylvanian and Guadalupian (Fig. 2). Furthermore, the results show that there is an increase in the sporomorph richness during the Gzhelian–Asselian transition followed by a decrease in the Kungurian–Roadian limit. In addition, a peak in richness is observed in the Moscovian, followed by a marked decrease during the Kasimovian and Gzhelian, previous to the increase at the Gzhelian–Asselian transition. However, there should be noted that the recovered richness pattern considerably follows the pattern observed for sampling, indicating a certain influence of sampling over the richness estimates. Nevertheless, when confidence intervals are considered, there is almost no overlap between the major changes in richness, indicating that the observed

changes are not entirely explained by sampling differences. In the majority of the time intervals, the estimated sampling probability was relatively high, with values over 0.85. Contrarily, the confidence interval for the Lopingian is considerably larger than the other periods, which is expected given the poor sampling for this interval and makes any assumptions regarding richness unreliable.

Furthermore, if spores and pollen grains are considered separately, some important differences are observed (Fig. 3). Although there is a common pattern in richness in both groups, spores show higher richness during the Pennsylvanian, whereas pollen grains increase in the Ghezelian–Asselian and during the Cisuralian, both groups maintain a similar richness. In the Guadalupian, the spore richness decreases in relation to the pollen grains, although in the latter case, the CI overlap is considerable. This inversion in the pattern of spore-pollen richness observed in Fig. 3 is not supported by sampling bias, as a similar pattern of sampling estimates was obtained.

Regarding the Inverse Survivorship Models, the results largely supported models with constant sampling, thus indicating that modeling different sampling rates for different intervals did not significantly improve model fit. This result further supports the fact that sampling effort in the present data is adequate and is not significantly different across time. On the other hand, models with constant origination and extinction rates showed extremely poor fits (Table 1), indicating that the data support the existence of significant changes in the origination and extinction dynamics of sporomorphs during the analyzed time
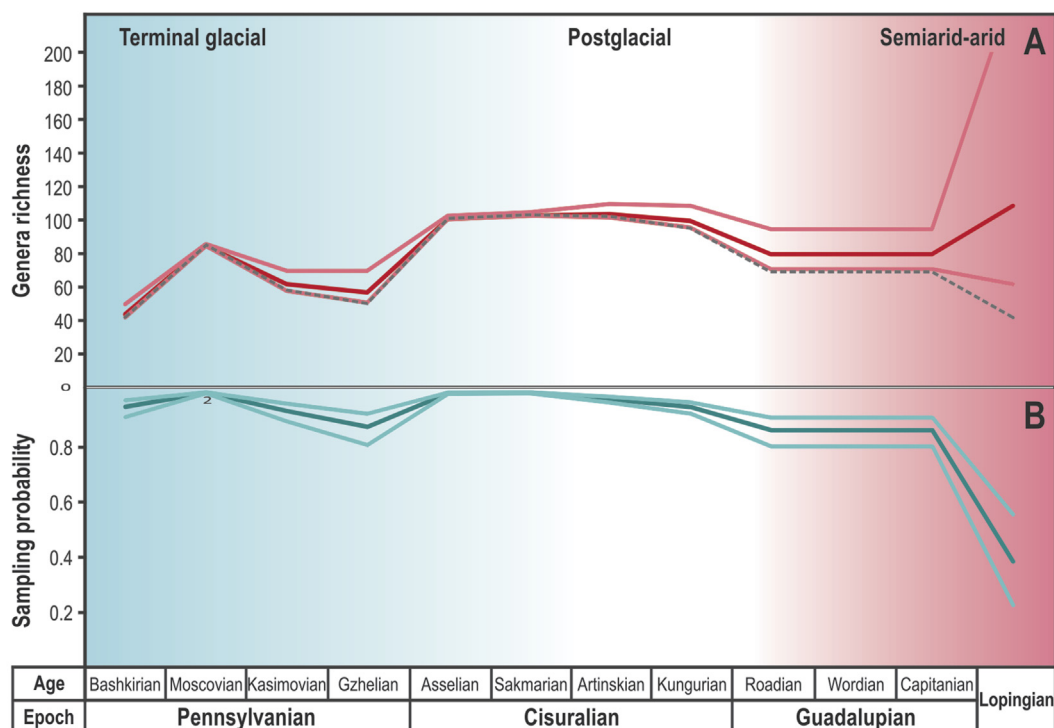
Fig. 2. True Richness (A) and sampling probabilities (B) with the respective 95% CI (lighter lines) based on recorded genera using the TRiPS method. Paleoclimatic stages according to Limarino et al. (2014). The dashed line represents raw count data.
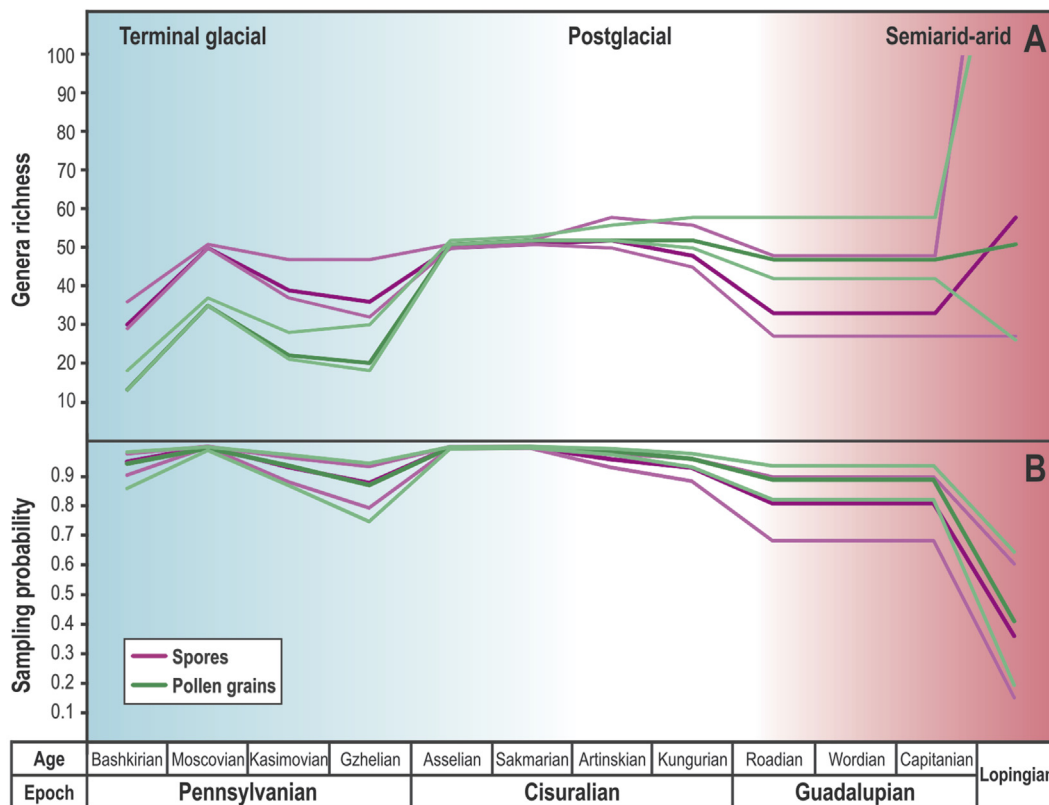
Fig. 3. True Richness (A) and sampling probabilities (B) with the respective 95% CI for spores and pollen grains based on recorded genera using the TRiPS method.
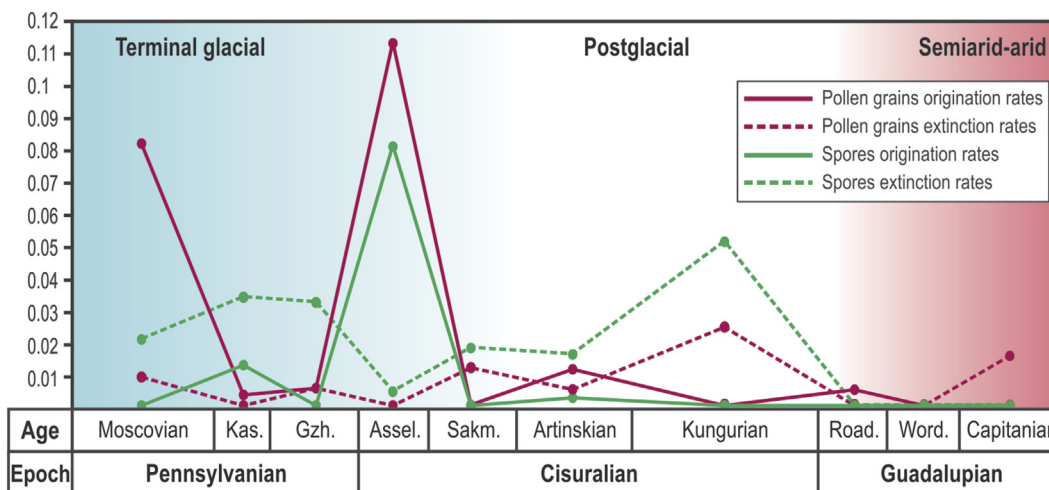

Fig. 4. Estimated origination and extinction rates based on the best fitted model (variable origination and extinction rates with constant sampling rate and spores and pollen grains considered separately) on the ISM analyses.

interval. Additionally, the model showed the best fit assumed variable origination and extinction rates for spores and pollen grains separately (Fig. 4). These results agree with the TRiPS results and further support differences in the diversity dynamics of spores and pollen grains. Overall, the best model showed the highest origination rates during the Asselian and the lowest origination rates during the Kungurian, whereas extinction rates showed peaks at the Kasimovian, Gzhelian, and Kungurian and were lower for the Asselian. Pollen grains showed higher or equal origination rates than spores except during the Kasimovian, and spores exhibited higher extinction rates than pollen grains except during the Guadalupian. In this sense, pollen grains showed higher net diversification than spores during the studied interval, and

spores showed higher turnover than pollen grains. These patterns are in accordance with the alternation of richness dominance observed in the TRiPS analysis, which is clearly related to the differential peaks in origination and extinction of spores and pollen grains in the Pennsylvanian–Cisuralian–Guadalupian transitions.

5. Discussion

The results obtained here are consistent with previous studies on the diversity of upper Paleozoic sporomorphs in the region (Beri et al., 2013b, 2015, 2018). These analyses, which were carried out in different strata and geographical locations and using different analysis tools,

show that the greatest diversity occurs in the Cisuralian. However, sampling effort in different strata and geographical locations is variable and can result in biases as important as to invalidate interpretations. For this reason, it is necessary to deepen studies aimed at assessing this potential weakness. In this aspect, modeling approaches can provide important insights regarding the potential biases in fossil data. In particular, a recent method developed by Starrfelt and Liow (2016) showed the importance of sampling biases in the study of the dinosaur fossil record and their extinction events. Likewise, Foote (2001) implemented methods based on survivorship analysis to study Paleozoic marine animals. These approaches permit the explicit modeling of sampling bias and, in the latter, hypothesis testing, allowing the statistical evaluation of sampling bias and the simultaneous testing of biological hypotheses concerning different origination-extinction dynamics or different patterns between taxonomic groups.

The results of the TRiPS analysis (Figs. 2 and 3) show an overall increase in sporomoprhs richness through the Pennsylvanian (although a clear loss is seen at its end), with the highest values occurring during the Cisuralian and a slight decrease occurring at the beginning of the Guadalupian. Importantly, sampling remains high for most of these time intervals, providing considerably accurate richness estimates. On the other hand, sampling quality is significantly reduced for the Lopingian (~40% sampling probability), and consequently, richness estimates become less accurate. In this case, any evaluation regarding sporomorphs richness during the Guadalupian-Lopingian transition is tentative, and more sampling should be available in order to address patterns in diversity during the late Permian and before the mass extinction. Interestingly, when considering spores and pollen grains separately, sampling quality for both groups remains almost equal, but differences in estimated richness are clearly evident. In particular, a shift in the dominant sporomorphs is observed during the Cisuralian, with spores being dominant during the Pennsylvanian and pollen grains becoming dominant in the Guadalupian, although in the latter case the confidence interval (CI) overlap is considerable.

Moreover, the Inverse Survivorship approach shows significant support for models with constant sampling, reinforcing the idea that sampling bias is low, and sampling can be considered homogeneous in the data. On the other hand, more complex models with variable origination and extinction rates are supported over constant rate models. In particular, the best-supported model considered different origination and extinction dynamics between spores and pollen grains. These results are in line with the TRIPS results, which showed mostly uniform sampling and different patterns of richness between both groups. Regarding these origination and extinction rates (Fig. 4), the estimated values show that spores extinction rates are higher than pollen rates for most of the studied time interval, whereas origination rates are higher for spores during the Pennsylvanian and higher for pollen grains during the Cisuralian and Guadalupian. This result is in agreement with the shift in richness obtained in the TRiPS analysis.

The observed patterns in diversity, extinction, and origination of spores in the late Palaeozoic are consistent with the evolution of global vegetation addressed by Cascales-Miñana et al. (2010, 2018) and Cleal and Cascales-Miñana (2014). A peak in global plant diversity occurs during the early–middle Pennsylvanian that progressively declines during Late Pennsylvanian and Permian times. Gradstein and Kerp (2012) and Stephenson (2016) indicate that, when considering Euramerican coal swamps, a replacement of arborescent lycophytes by arborescent tree ferns took place near the end of the Carboniferous, being one of the most important changes in land plants. This pattern is consistent with our findings for Western Gondwana, which show that spores become replaced by pollen grains at the beginning of the Permian. However, this replacement did not probably occur on a global scale, and knowledge regarding these groups in Gondwana is still limited. The palynological data also show a small decrease in the number of spore genera in the Carboniferous–Permian boundary and an increase in the Cisuralian, when a wide variety of pteridophytes and new

seed plant groups appeared (e.g., cycads, ginkgos, voltzialean, conifers, and glossopterids), and became important in the Permian of Gondwana (hundreds of species). It is estimated that by the late Permian, approximately 60% of the world's flora consisted of seed plants, suggesting that major changes occurred during the Permian (Cascales-Miñana et al., 2010, 2018). Therefore, the observed increase in the diversity of pollen grains genera in the Asselian revealed in our study is expected. At the end of the ice age in the late Cisuralian–Guadalupian, another significant decrease in global plant diversity is documented. Iannuzzi (2013) indicated that the diversity of different megafloral groups in Brazil exhibits peaks in the Asselian/Artinskian and the Wordian/Wuchiapingian.

On the other hand, there is a relationship between richness, extinction, and origination processes observed in sporomorphs and climatic conditions. Limarino et al. (2014) recognized four major paleoclimatic stages for the southern South American basins during the late Paleozoic: 1) glacial (late Visean–early Bashkirian), 2) terminal glacial (Bashkirian–earliest Cisuralian), 3) post-glacial (Cisuralian–early Guadalupian), and 4) arid-semiarid (late Guadalupian–Lopingian). Considering the results of the present study, at the beginning of the Cisuralian, during the postglacial stage, there is a clear increase in diversity that is maintained for most of the interval supported by high sampling probabilities and narrow confidence intervals in richness estimates (Figs. 2–4). Furthermore, origination rates are very high, whereas extinction rates are very low, whether total genera are taken into account or if spores and pollen grains are considered separately. Therefore, this pattern could be related to an increase in plant diversity in response to climatic amelioration. In turn, the highest extinction rates are observed in the Kungurian, both in spores and pollen grains, indicating that vegetational changes occurred at the onset of the arid-semiarid stage.

Finally, it is important to take into account that some differences could exist between the Pacific and Atlantic basins. Limarino et al. (2014) proposed that at the same climatic stage, different basins present differences in their evolution. For example, in the terminal glacial stage, till deposits, diamictites, and striated pavements are presented in the Atlantic basins, while these features are not observed in the Pacific basins. In addition, the palynological information included in our database was not homogeneously distributed over time. Palynofloras from the Pacific basins cover times not younger than Sakmarian–Artinskian, whereas a wider range (Cisuralian–Lopingian) is documented for the Atlantic basins. Furthermore, the data from the Paganzo Basin used in the current analysis are fewer than those of the other basins. This inequality in the density of information between the studied basins could restrict the extension of the conclusions to the western margin of Gondwana, particularly in relation to the Paganzo basin. All these issues could represent limitations regarding the overall patterns obtained from the data and should be the subject of future approaches. Despite the limitations related to different types of biases, the results show some coherence with the models proposed for both climatic and vegetation evolution, mostly for South America. Although it is not the subject of the present work, fossil palynomorphs have been shown to represent a powerful tool for the definition of biostratigraphic proposals. However, palynology can also represent a useful tool for the study of diversity patterns in the past, especially considering its extensive fossil record.

6. Conclusions

Changes in total sporomorph diversity, as well as differences between spores and pollen grains, are directly related to changing climatic conditions in Western Gondwana during the late Paleozoic that could impact differently over plant communities.

Although the fossil palynomorph record is commonly used as a biostratigraphic tool, our results highlight its importance and usefulness for the study of plant communities and their evolution in the past. Further modeling approaches accounting for different potential biases

and statistically testing different hypotheses should greatly improve our understanding of the observed patterns in Paleozoic sporomorphs diversity and provide new insights regarding the evolution of floras during this period of the Earth's history.

CRediT authorship contribution statement

Ángeles Beri: Conceptualization, Data curation, Writing - original draft. **Ximena Martínez-Blanco:** Conceptualization, Data curation, Writing - original draft, Visualization. **Luciano Varela:** Conceptualization, Formal analysis, Writing - original draft. **Mercedes di Pasquo:** Resources, Data curation, Writing - review & editing. **Paulo Alves de Souza:** Resources, Data curation, Writing - review & editing.

Acknowledgment

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jsames.2019.102457.

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