Permian–Triassic land-plant diversity in South China: Was there a mass extinction at the Permian/Triassic boundary?

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Permian–Triassic land-plant diversity in South China: Was there a mass extinction at the Permian/Triassic boundary?

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Abstract.—Diversity dynamics of the Permian–Triassic land plants in South China are studied by analyzing paleobotanical data. Our results indicate that the total diversity of land-plant megafossil genera and species across the Permian/Triassic boundary (PTB) of South China underwent a progressive decline from the early Late Permian (Wuchiapingian) to the Early-Middle Triassic. In contrast, the diversity of land-plant microfossil genera exhibited only a small fluctuation across the PTB of South China, showing an increase at the PTB. Overall, land plants across the PTB of South China show a greater stability in diversity dynamics than marine faunas. The highest extinction rate (90.91%) and the lowest origination rate (18.18%) of land-plant megafossil genera occurred at the early Early Triassic (Induan), but the temporal duration of the higher genus extinction rates (>60%) in land plants was about 23.4 Myr, from the Wuchiapingian to the early Middle Triassic (Anisian), which is longer than that of the coeval marine faunas (3–11 Myr). Moreover, the change of genus turnover rates in land-plant megafossils steadily fluctuated from the late Early Permian to the Late Triassic. More stable diversity and turnover rate as well as longer extinction duration suggest that land plants near the PTB of South China may have been involved in a gradual floral reorganization and evolutionary replacement rather than a mass extinction like those in the coeval marine faunas.

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Introduction

Paleobiodiversity change (i.e., the change of taxonomic diversity through geological time) can provide substantial insight into the tempo and mode of macroevolution in the history of life, so the statistical analysis of paleobiodiversity has increasingly become one of the central themes in paleobiology (Raup 1972; Valentine 1985; Raup and Jablonski 1986; Benton 1995; Adrain and Westrop 2000; Jackson and Johnson 2001; Bambach 2006; Hammer and Harper 2006; Ruban and van Loon 2008). In paleobiodiversity studies mass extinction events are the most conspicuous and have attracted extensive attention from paleobiologists, geologists, and conservation biologists. In the past decades, representative analytical results have been published on faunal diversity and mass extinctions through geological time, such as the ''big five'' mass extinctions among marine invertebrates and vertebrates (Raup and Sepkoski 1982) and mass extinctions among non-marine tetrapods (Benton 1985). In contrast, the iconic results about the response (or relationship) of land-plant diversity to mass extinctions are still uncertain and controversial, though numerous studies on floral diversity change through time have been undertaken. To date, it remains elusive whether land plants have undergone mass extinctions and, if so, whether these catastrophes coincided with mass extinctions in animals (e.g., Niklas et al. 1983, 1985; Knoll 1984; Traverse 1988, 2007; Wang 1989; Raymond and Metz 1995; Willis and Bennett 1995; Wing and DiMichele 1995; Niklas 1997; Rees 2002; Willis and McElwain 2002; Wing 2004; Goman'kov 2005; Grauvogel-Stamm and Ash 2005; McElwain and Punyasena 2007; Ruban and van Loon 2008).

The Permian/Triassic boundary (PTB) mass extinction was the most devastating event to impact life on Earth. It has been estimated that 94–98% of species, 82–84% of

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genera, and 51–57% of families in marine faunas died out in the PTB mass extinction (Raup and Sepkoski 1982; Jablonski 1991; Raup 1994; Erwin 1998; Benton and Twitchett 2003). In South China, 94% of species, 90% of genera, 80% of families, and 75% of orders in marine faunas became extinct in the PTB mass extinction (Jin et al. 2000b; Rong and Fang 2004; Rong et al. 2006). However, whether a synchronous mass extinction occurred in land plants at the PTB is still controversial (Knoll 1984; Dobruskina 1987; Traverse 1988; Wang 1989, 1992; Li 1994; Retallack 1995; Banerji 1997; Niklas 1997; Peng et al. 2001; Twitchett et al. 2001; Rees 2002; Willis and McElwain 2002; Fang 2004; Goman'kov 2005; Grauvogel-Stamm and Ash 2005; Zhu and Ouyang 2005; McElwain and Punyasena 2007; Xiong and Wang 2007). At present, evolutionary replacement and mass extinction are the two competing hypotheses to explain land-plant diversity dynamics at the PTB.

The main purposes of this paper are (1) to study the diversity dynamics of Permian–Triassic land plants in South China, (2) to compare the changing diversity patterns between the coeval faunas and floras, and (3) to test previous hypotheses.

International Stratigraphic Chart (Gradstein et al. 2004)			Intervals-Ma (Present paper)	
Triassic	Upper	Rhaetian	N_2-Rh	199.6
		Norian		210.05
		Carnian	Cr-N_1	
	Middle	Ladinian	L	228.0
		Anisian	An	237.0
	Lower	Olenekian	O	245.0
		Induan	I	249.7
Permian	Lopingian	Changhsingian	Ch	251.0
		Wuchiapingian	Wu	253.8
	Guadalupian	Capitanian	Wo-Ca	260.4
		Wordian		
		Roadian	Ku-Ro	268.0
	Cisuralian	Kungurian		
		Artinskian	As-Ar	275.6
		Sakmarian		
		Asselian		299.0

FIGURE 1. Division of stratigraphic intervals of land plants during the Permian–Triassic of South China.

Data

Data Sources.—The data are compiled from the existing literature on the Permian–Triassic land plants in South China. We have compiled the data since September 2006 and preliminarily finished this database in January 2009. Currently, the database encompasses 315 genera and 1371 species of land plants from the Permian–Triassic of South China. The data for each species are derived directly from an original literature citation, and secondary sources have been used to correlate with the original literature. All the original data are available online (see Supplementary Material at http://dx.doi.org/10.1666/09029.s1). This contribution represents a portion of the senior author's dissertation, submitted to the Institute of Botany, the Chinese Academy of Sciences (Xiong 2009).

Stratigraphic Intervals.—The stratigraphic section comprising the Permian–Triassic flora of South China has been subdivided into ten stratigraphic intervals: four in the Permian and six in the Triassic (Fig. 1), which can be correlated with the stratigraphic subdivisions of the International Stratigraphic Chart (Gradstein et al. 2004). Prior to the Kungurian, there are only marine sediments in the Early Permian of South China (Jin et al. 2000a), and the previously reported floras in the early Early Permian should be considered as ranging from the Kungurian to the Roadian. Overall, we actually study the land-plant diversity from the Kungurian to the Rhaetian (end-Triassic).

Taxonomic Compilations.—Our database of Permian–Triassic land plants in South China includes megafossils and microfossils (i.e., spores and pollens), which serve as cross-references for a general pattern of floral diversity dynamics. The lowest taxonomic rank is species. Compared with higher taxa, species often yield more synonyms and *incertae sedis*, so we mainly analyzed the extinction, origination, and turnover rates at the genus level. Paleobotanical genera sometimes are difficult to attribute to family, so we adopted Wang's (1989) scheme to classify the

TABLE 1. Genus number of land-plant megafossils and total diversity of land-plant megafossils and microfossils through the Permian–Triassic of South China (number of species in parentheses).

Taxonomic groups	Ku–Ro	Wo–Ca	Wu	Ch	I	O	An	L	$Cr–N_1$	N_2–Rh
Ferns	1 (3)	14 (63)	23 (124)	14 (38)	1 (1)	2 (2)	2 (2)	1 (1)	38 (135)	31 (145)
Sphenopterids	0 (0)	2 (10)	3 (14)	2 (3)	0 (0)	0 (0)	0 (0)	0 (0)	3 (8)	3 (9)
Pecopterids	1 (3)	9 (48)	9 (86)	6 (26)	1 (1)	0 (0)	1 (1)	1 (1)	2 (25)	3 (43)
Eusporangiate ferns	0 (0)	1 (2)	4 (16)	3 (4)	0 (0)	1 (1)	0 (0)	0 (0)	9 (29)	6 (17)
Leptosporangiate ferns	0 (0)	1 (1)	2 (3)	1 (2)	0 (0)	1 (1)	1 (1)	0 (0)	13 (60)	13 (66)
Other taxa	0 (0)	1 (2)	5 (5)	2 (3)	0 (0)	0 (0)	0 (0)	0 (0)	11 (13)	6 (10)
Noeggerathiopsids	1 (1)	3 (3)	4 (11)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Lycopsids	2 (6)	5 (9)	7 (20)	7 (15)	3 (8)	1 (1)	2 (7)	2 (6)	2 (3)	3 (3)
Sphenopsids	1 (1)	11 (31)	15 (52)	6 (16)	4 (4)	3 (6)	3 (4)	2 (3)	7 (30)	10 (47)
Gymnosperms	3 (3)	25 (62)	49 (144)	28 (47)	3 (4)	21 (28)	14 (22)	7 (7)	70 (324)	76 (357)
Primitive gymnosperms	2 (2)	16 (49)	22 (79)	11 (24)	2 (3)	3 (3)	2 (2)	0 (0)	4 (11)	2 (3)
Gigantopterids	2 (2)	8 (29)	11 (49)	3 (11)	2 (3)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Neuropterids	0 (0)	2 (4)	2 (7)	2 (4)	0 (0)	1 (1)	1 (1)	0 (0)	0 (0)	0 (0)
Callipterids	0 (0)	0 (0)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Odontopterids	0 (0)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Alethopterids	0 (0)	2 (5)	3 (14)	2 (3)	0 (0)	0 (0)	1 (1)	0 (0)	2 (9)	1 (1)
Cordaitopsids	0 (0)	2 (5)	3 (5)	2 (4)	0 (0)	1 (1)	0 (0)	0 (0)	1 (1)	0 (0)
Glossopterids	0 (0)	1 (5)	2 (3)	2 (2)	0 (0)	1 (1)	0 (0)	0 (0)	1 (1)	1 (2)
Advanced gymnosperms	0 (0)	4 (5)	15 (40)	8 (12)	1 (1)	16 (21)	9 (16)	6 (6)	51 (251)	62 (305)
Coniferopsids	0 (0)	0 (0)	2 (2)	3 (3)	0 (0)	10 (15)	4 (8)	0 (0)	13 (22)	17 (50)
Cycadopsids	0 (0)	1 (1)	3 (10)	1 (1)	0 (0)	4 (4)	2 (3)	3 (3)	33 (201)	31 (206)
Ginkgopsids	0 (0)	2 (2)	8 (26)	3 (7)	0 (0)	0 (0)	0 (0)	2 (2)	5 (28)	14 (49)
Peltasperms	0 (0)	1 (2)	2 (2)	1 (1)	1 (1)	2 (2)	3 (5)	1 (1)	0 (0)	0 (0)
Other taxa	1 (1)	5 (8)	12 (25)	9 (11)	0 (0)	2 (4)	3 (4)	1 (1)	15 (62)	12 (49)
Incertae sedis	0 (0)	6 (9)	19 (39)	5 (9)	0 (0)	0 (0)	0 (0)	1 (1)	6 (8)	5 (6)
Total diversity (megafossil)	8 (14)	64 (177)	117 (390)	61 (126)	11 (17)	27 (37)	22 (36)	13 (18)	123 (500)	125 (556)
Total diversity (microfossil)	83	64	114	70	102	49	85	59	151	242

genera into six major taxonomic groups: ferns, noeggerathiopsids, lycopsids, sphenopsids, primitive gymnosperms, and advanced gymnosperms, including more than 20 smaller taxonomic groups (Table 1). For convenience, the primitive gymnosperms and advanced gymnosperms mainly represent the Paleozoic and Mesozoic genera, respectively. A few taxa, e.g., *Rhizomopsis* Gothan et Sze, are referred to *other taxa* in the ferns; *Carpolithus* Brongniart is referred to *other taxa* in the primitive and advanced gymnosperms. *Incertae sedis* represents the taxa that cannot be referred to any group. The attribution of these smaller taxonomic groups is primarily based on the *Index Nominum Genericorum* (ING) (available at *http://botany.si.edu/ing/*).

Methods

Diversity Measures.—In order to measure the diversity dynamics of land plants across the PTB of South China, we calculated total diversity, standing diversity, and diversity per million years (Myr) at each time interval for species and genera.

Total diversity (Ti) is the total number of a given taxonomic rank within one time interval, which can be used to measure the number of genera or species of land-plant megafossils or microfossils encountered across the PTB of South China. However, the number of taxa present at any one time within an interval depends heavily on their actual durations (Harper 1996), and within any given interval some taxa will originate and others will disappear. Standing diversity, rather than total diversity, is therefore a preferable measure of diversity for any particular interval. The standing diversity (Tmi) is the number of taxa present at any one time (Ti) minus the half of the number of both genus originations (Oi) and extinctions (Ei) in the given time interval (Harper 1975). Thus, $Tmi = Ti - Oi/2 - Ei/2$.

Because all time intervals are not of equal duration, analyzing diversity regardless of the span of a time interval may distort the actual duration of the taxa within each time interval (Foote 1994; MacLeod and Keller 1994; Shen et al. 2004; Ruban and van Loon

2008). Therefore, we use diversity per million years to eliminate this possible bias. Diversity per million years is the ratio of total diversity (Ti) or standing diversity (Tmi) to the time interval duration: Ti/Myr or Tmi/Myr.

Origination and Extinction Rate Measures.—In order to measure the rate of evolution among Permian–Triassic land plants in South China, we calculate the genus origination and extinction rates, genus origination and extinction rates per million years, and the standing genus origination and extinction rates. The genus origination and extinction rates (OR and ER) are the ratios of the number of genus originations (Oi) and extinctions (Ei) to the total number of genera (Ti) within one time interval. Thus, OR = Oi/Ti, and ER = Ei/Ti. We can then calculate the origination and extinction rates per million years by dividing this by the number of Myr in the time interval.

Not all taxa are present at any time within one interval, so we use the standing origination and extinction rates (SOR and SER) of land-plant genera (Gilinsky 1991): $SOR = [(Oi - Ci)/Tmi]/2$, where $0 \leq SOR \leq 1$; $SER = [(Ei - Ci)/Tmi]/2$, where $0 \leq SER \leq 1$. Here, Ci is the number of singletons, representing the number of genera that occur only in a particular time interval.

Turnover Rate Measures.—The genus turnover rates are the correlation values between extinction and origination rates, which reflect the amount of change in biotic composition through time (Shen et al. 2004; Meloro et al. 2008). In our analysis, turnover rate (TuR) mainly elucidates the degree of floral change and reorganization across the PTB of South China. It can be expressed by the equation $TuR = OR + ER - Ci/Ti$.

Polynomial Regression Analysis.—Paleobiodiversity studies suggest that sampling intensity (or the number and size of samples) has a strong effect on the total measured diversity of land plants (Raymond and Metz 1995; Rees 2002; Wing 2004). To evaluate the effect of sampling intensity, we use polynomial regression analysis to examine the correlation between the expected diversity of megafossil and microfossil genera and the number of localities at which they are found across the PTB of South China. The free software package PAST was used for the polynomial regression analysis (Hammer 1999–2009; available at *http://folk.uio.no/ohammer/past/*).

Results

Genus and Species Diversity.—The total diversity of megafossil land-plant genera and species across the PTB of South China is listed (Table 1). Two diversity curves of megafossils (Fig. 2), showing total genus and species diversity, undergo a similar pattern of change. Overall, the diversity of land-plant megafossil taxa increases from the Kungurian to the Wuchiapingian, declines from the Wuchiapingian to the Induan, remains low until the Ladinian, and then increases in the Late Triassic. However, diversity dynamics of microfossil genera show a different pattern of change, increasing from the Wordian to the Wuchiapingian, decreasing at the Changhsingian (end-Permian), and rising at the PTB (Fig. 2). The lowest value of diversity lies in the Olenekian. Overall, the diversity of microfossil genera is higher than for megafossils in the Early–Middle Triassic, showing repeated small declines throughout the Middle Permian to Middle Triassic of South China.

The values of genus and species diversity per million years decline progressively from the Wuchiapingian to the Middle Triassic. The lowest values of both genus and species diversity per million years occur in the Ladinian (Table 2, Fig. 3).

Origination, Extinction, and Turnover Rates.—Table 3 and Figure 4 present genus origination, extinction, and turnover rates, species extinction rate, standing genus origination and extinction rates, and genus origination and extinction rates per million years in land-plant megafossils across the PTB of South China. The lowest genus origination rate (18.18%) occurs in the Induan and the highest value (96.30%) in the Olenekian. In contrast, genus extinction rate, standing genus extinction rate, and genus extinction rate per million years are lower in the Wordian–Capitanian and the Late Triassic. The highest values, 90.91% and 94.12% respectively, of genus and species extinction rates are in the

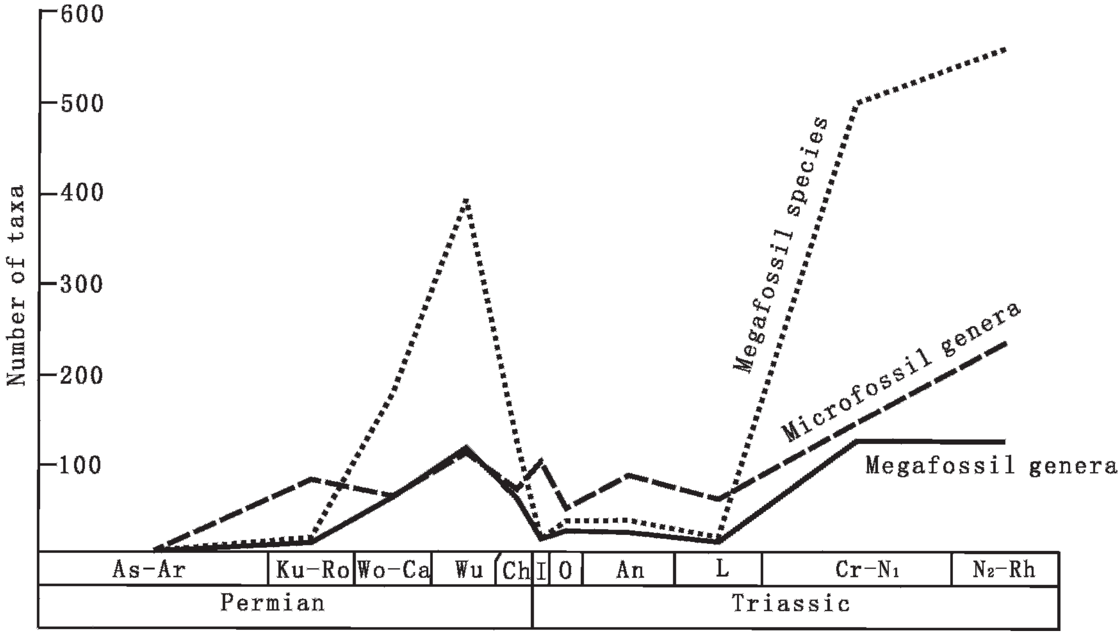

FIGURE 2. Diversity of land-plant taxa across the PTB of South China.

Induan. High extinction rates for genera (>60%) and species (>80%) occur from the Wuchiapingian to the Anisian, a duration of 23.4 Myr.

High genus turnover rates occur in the Wordian–Capitanian, the Induan, the Olenekian, and the Anisian, ranging from 90.91% to 99.99%, with the highest in the Induan. Overall, genus turnover rates fluctuated throughout the Permian and Triassic.

Effect of Sampling Intensity.—The greater the sampling intensity, the higher is the diversity within a floral assemblage. Hence, it is not surprising that fewer land-plant species have been reported from the early Early Permian and the early Early Triassic, because fewer localities are known from these intervals. Our polynomial regression analysis shows a positive correlation between the expected number of megafossil and microfossil genera and the number of localities (Fig. 5A). The expected genus diversity (Fig. 5B) appears, to some extent, similar to the observed genus diversity of land plants across the PTB of South China (see Fig. 2).

Discussion

Diversity Comparisons between Coeval Floras and Faunas.—Diversity dynamics of land-plant megafossil genera in North China do

TABLE 2. Diversity, origination, and extinction of land-plant megafossils across the PTB of South China.

	Genus standing diversity per Myr	Species diversity per Myr	Genus diversity per Myr	Genus extinctions	Genus originations	Number of singletons	Genus standing diversity
Ku–Ro	0.5263	1.8421	1.0526	4	4	3	4
Wo–Ca	3.6184	23.2895	8.4211	13	60	13	27.5
Wu	7.197	59.0909	17.7273	72	67	48	47.5
Ch	9.2857	45	21.7857	53	17	17	26
I	3.8462	13.0769	8.4615	10	2	1	5
O	1.0638	7.8723	5.7447	18	26	18	5
An	1.0625	4.5	2.75	14	13	7	8.5
L	0.9444	2	1.444	4	5	1	8.5
Cr–N_1	2.4513	27.8552	6.8524	44	114	44	44
N_2–Rh	7.3206	53.2057	11.9617	51	46	26	76.5

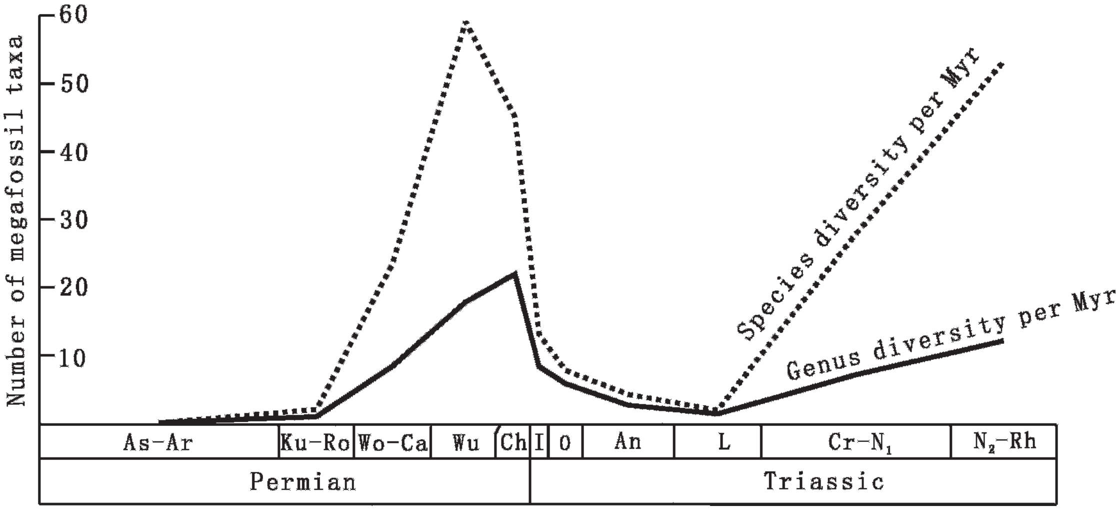

FIGURE 3. Genus and species diversity per million years of land-plant across the PTB of South China.

not show dramatic change from the early Early Permian to the early Late Permian, but there is a sharp decline from the late Late Permian (Changhsingian) to the early Early Triassic (Induan) (Wang 1989; Rees 2002) (Fig. 6). Overall, diversity dynamics of land-plant genera across the PTB of South China are noticeably different from those of the coeval Angara, Euramerica, Gondwana, and North China (Rees 2002). Our results are generally similar to Rees's (2002) curve.

Diversity of marine faunas across the PTB of South China has been studied in detail (Jin et al. 2000b; Rong et al. 2006) (Fig. 6). Marine faunas undergo multi-staged diversity depletions in the terminal stage of the early Early Permian (Artinskian), the early Late Permian (Capitanian), the early Early Triassic (Induan), the Middle Triassic (Ladinian), and the Late Triassic (Rhaetian). The lowest diversity of marine faunas occurs in the Induan. Taxonomic recovery of marine faunas and tetrapods after the PTB crisis is rapid in the late Early Triassic and the early Middle Triassic (Erwin 1998; Rong and Fang 2004; Rong et al. 2006; Sahney and Benton 2008), but diversity begins to decline thereafter, throughout the Triassic.

Although land plants in South China similarly show lowest diversity in the Induan, the increasing diversity in plant microfossil genera at the PTB, as well as the higher diversity in the Early–Middle Triassic of South China (Table 1, Fig. 2), suggests that the depletion of land plants across the PTB is not as dramatic as that of marine animals. Genus and species diversity per million years in megafossil taxa do not bottom out until the Middle Triassic

TABLE 3. Origination, extinction, and turnover rates of land-plant megafossils across the PTB of South China.

	Genus origination rates	Genus (species) extinction rates	Genus origination rates per Myr	Genus extinction rates per Myr	Standing genus origination rates	Standing genus extinction rates	Genus turnover rates
Ku–Ro	0.5	0.5 (0.7557)	0.0658	0.0658	0.125	0.125	0.625
Wo–Ca	0.9375	0.2031 (0.3898)	0.1234	0.0267	0.8545	0	0.9375
Wu	0.5726	0.6154 (0.8051)	0.0868	0.0932	0.2	0.2526	0.7777
Ch	0.2787	0.8689 (0.9286)	0.0995	0.3103	0	0.6923	0.8689
I	0.1818	0.9091 (0.9412)	0.1398	0.6993	0.1	0.9	0.9999
O	0.9630	0.6667 (0.8919)	0.2049	0.1419	0.8	0	0.9630
An	0.5909	0.6364 (0.8889)	0.0739	0.0796	0.3529	0.4118	0.9091
L	0.3846	0.3077 (0.6111)	0.0427	0.0342	0.2353	0.1765	0.6154
Cr–N_1	0.9268	0.3577 (0.518)	0.0516	0.0199	0.7955	0	0.9268
N_2–Rh	0.368	0.408 (—)	0.0352	0.039	0.1307	0.1634	0.568

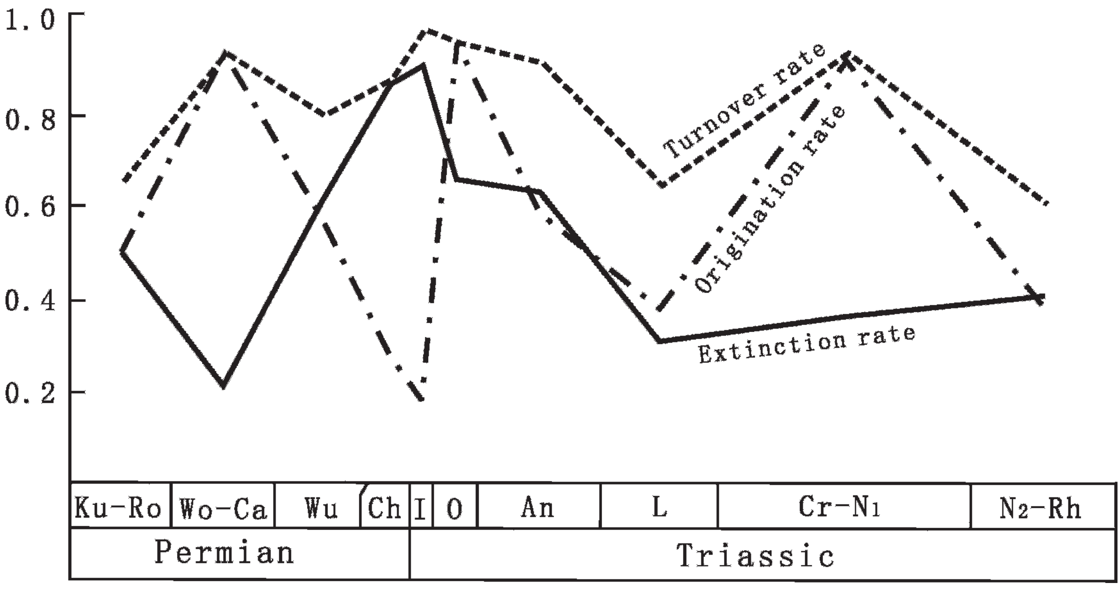

FIGURE 4. Extinction, origination, and turnover rates of land-plant megafossil genera across the PTB of South China.

(Ladinian), implying that the decrease of land-plant diversity across the PTB is progressive. Similarly, Niklas (1997) indicated that the highest extinction rate in land-plant species across the PTB occurs at the Middle Triassic (Anisian). Rees's (2002) study of land-plant diversity across the PTB in Angara, Euramerica, Gondwana, North China, and South China suggested that each floral province has a different extinction pattern, and that the lowest diversity of land-plant genera in South China occurs in the Middle Triassic. Our results show the diversity dynamics of land plants in South China were more stable than those of the coeval marine faunas. The total diversity and standing diversity of land-plant megafossil genera and species across the PTB of South China underwent a progressive decline from the Wuchiapingian to the Induan, and then kept a very low value until the Ladinian. Compared with the marine faunas, it took a longer time for land plants to survive and recover in the Early–Middle Triassic. Subsequently, land plants underwent a dramatic adaptive radiation in the Late Triassic while marine faunas declined in diversity. Overall, land plants across the PTB of South China were involved in a macroevolutionary pattern of crisis: extinction–survival–recovery–radiation.

The diversity disparity between land plants and marine faunas across the PTB of South China implies that the ultimate causes and the modes of response to the high extinction rates are not entirely the same for land plants and marine faunas. Wing (2004) suggested that extinctions largely affect lower taxonomic levels among plants than they do among marine organisms or vertebrates. As macroscopic autotrophic primary producers, land plants boast more diverse endemic taxa, survival strategies, and habitats (Traverse 1988; Valentine et al. 1991; Benton 2001). These characteristics may have provided a stronger survivability and helped buffer land plants against the catastrophic events at the PTB.

Evolutionary Replacement versus Mass Extinction.—Mass extinction has been defined as "any substantial increase in the amount of extinction (i.e., lineage termination) suffered by more than one geographically wide-spread higher taxon during a relatively short interval of geologic time, resulting in an at least temporary decline in their standing diversity" (Sepkoski 1986: p. 278). However, Bambach (2006) suggested that this definition of the term *mass extinction* obscures a number of details. To fully understand the nature of land-plant extinction at the PTB of South

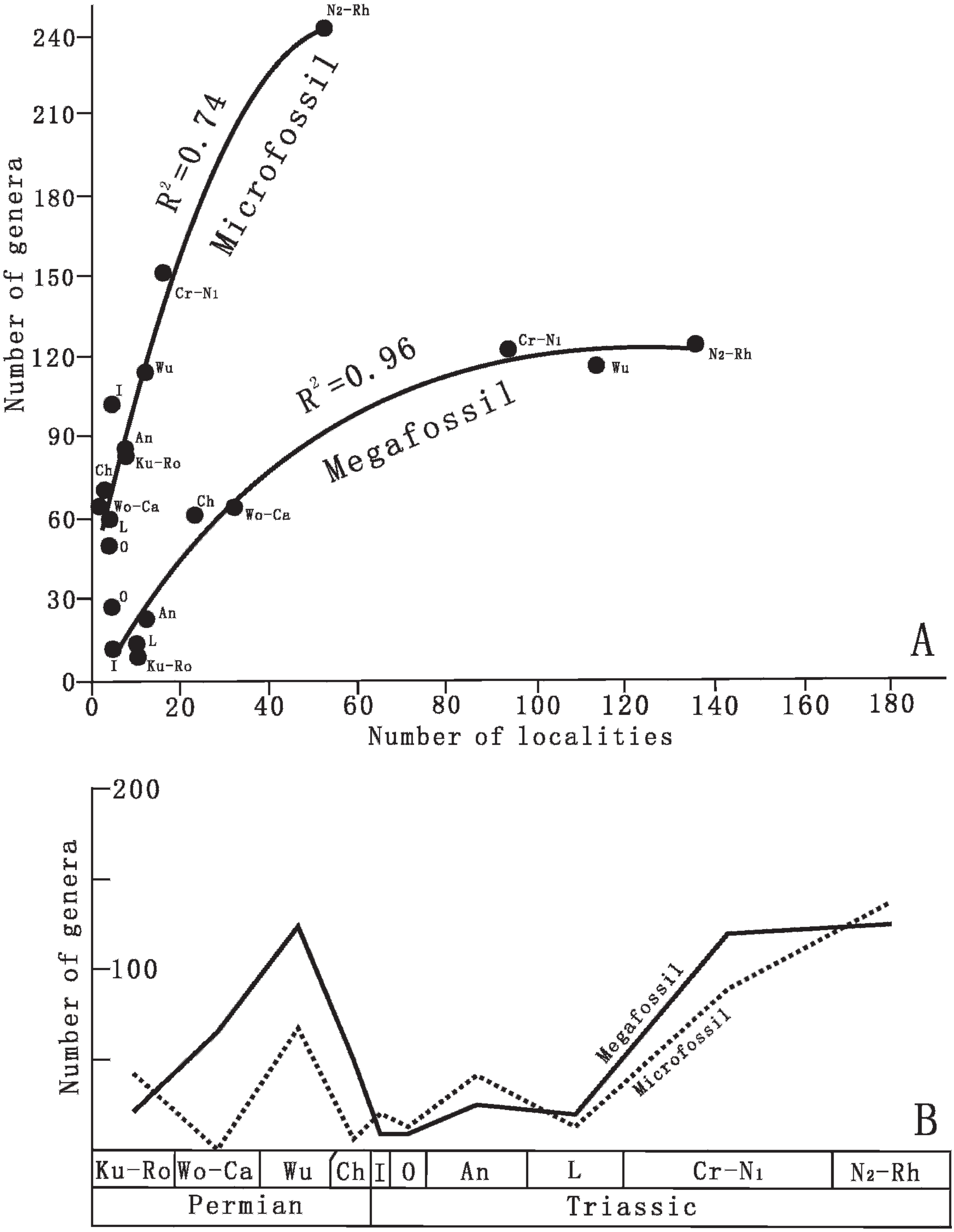

FIGURE 5. A, Regression curves of the expected number of megafossil and microfossil genera based on the number of localities in the Permian and Triassic of South China. B, Expected diversity of megafossil and microfossil genera in the Permian and Triassic of South China (based on the regression in A).

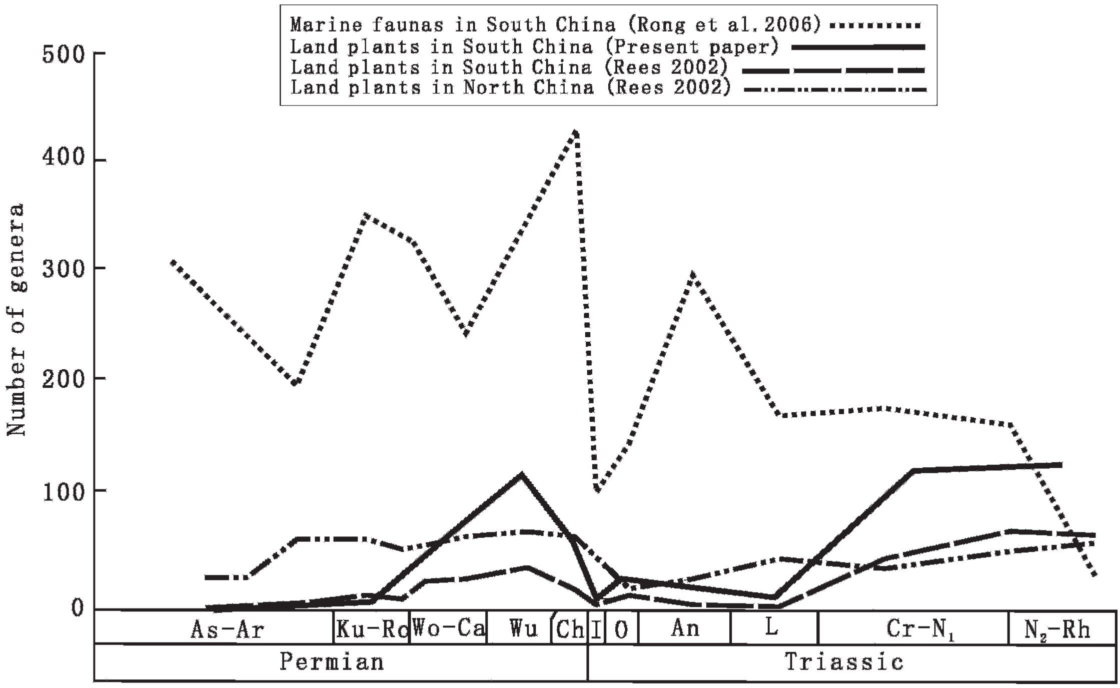

FIGURE 6. Comparisons of genus diversity between the Permian–Triassic floras and faunas in China.

China, it is therefore necessary to discuss the magnitude, extent, breadth, and duration, which are four key traits used to define a mass extinction (Flessa et al. 1986). Thus, a mass extinction should have the following traits in common: substantial magnitude, global extent, broad taxonomic effect, and relatively short temporal duration.

Our results show that the highest extinction rate (90.91%) and the lowest origination rate (18.18%) of land-plant megafossil genera of South China occur in the Induan, but genus extinction rates in neighboring time intervals are generally higher. The duration of the higher genus extinction rates (>60%) in land plants is about 23.4 Myr, from the Wuchiapingian to the Anisian. Likewise, the species extinction rates abruptly rise from 38.98% in the Wordian–Capitanian to 80.51% in the Wuchiapingian, and the following four time intervals from the Changhsingian to the Anisian have values of 92.86%, 94.12%, 89.19% and 88.89%, which are obviously higher than those of other time intervals (30–70%). The substantial magnitudes in extinction rates lead to a continuous diversity decline in land plants from the Wuchiapingian to the Anisian of South China, which last for about 23.4 Myr. Therefore, the extinction pattern and temporal duration of land plants near the PTB of South China are evidently different from those of coeval marine faunas, which have mass extinctions with a shorter duration, only 3–8 Myr (Schubert and Bottjer 1995) or 11 Myr (Erwin 1998).

The highest genus turnover rates (>90%) of land plants across the PTB of South China occur in the Wordian–Capitanian, Induan, Olenekian, and Anisian, but the turnover rate fluctuates from the late Early Permian to the Late Triassic. High turnover rate indicates massive biotic alteration and ecosystem rearrangement (Meloro et al. 2008). Prior to the PTB, land plants in South China are dominated by ferns, lycopsids, sphenopsids, and primitive gymnosperms (Fig. 7). From the Changhsingian to the Late Triassic, a gradual transition occurs, with the reduction and eventual extinction of Paleozoic groups, and the emergence and major radiation of Mesozoic ferns and advanced gymnosperms, lasting for about 30 Myr.

Some paleobotanists have suggested that the evolution of land plants across the PTB

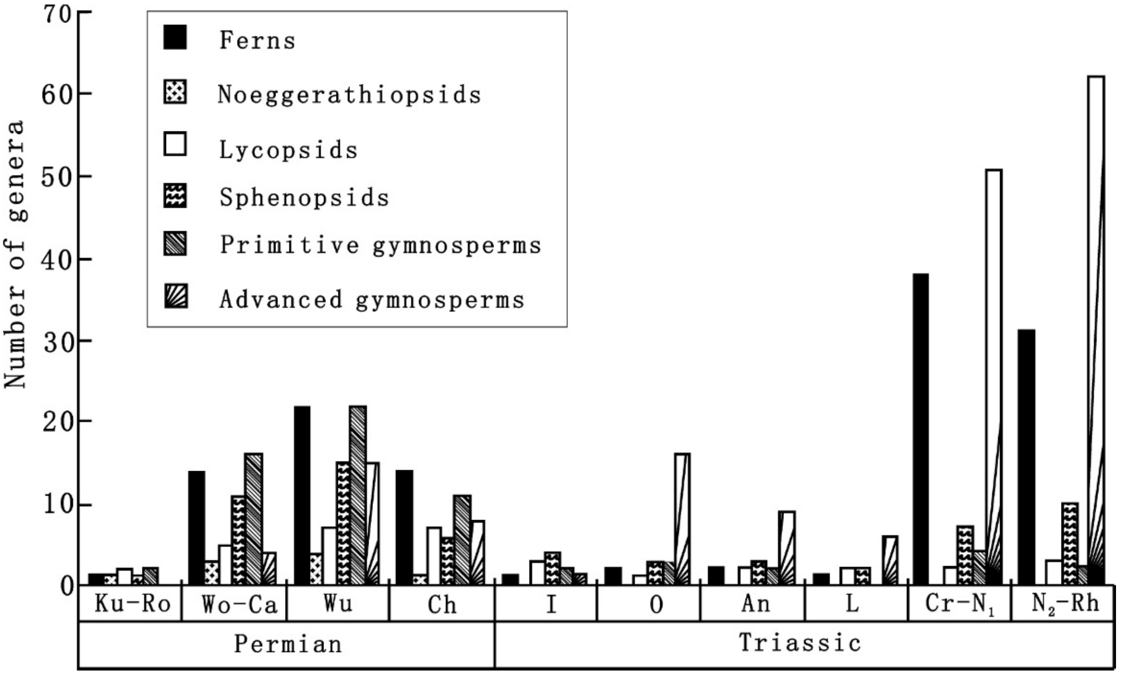

FIGURE 7. Macroevolutionary pattern of major taxonomic groups across the PTB of South China.

involved a gradual and long-term reorganization of major floristic elements (e.g., Knoll 1984; Traverse 1988, 2007; Wang 1992; Banerji 1997; Goman'kov 2005; Xiong and Wang 2007). The high turnover rates, long duration of decline in diversity, and subsequent relative stability following the emergence of new groups all suggest that land plants near the PTB of South China may have been involved in an evolutionary replacement, rather than a mass extinction like that in the coeval marine faunas.

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