



Modern pollen distribution in the northeastern Indian Ocean and its significance

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Abstract

In order to provide a reference for reconstructing the paleoclimate of the northeastern Indian Ocean, 36 airborne pollen samples were analyzed using methods for airborne pollen, and 26 surface water samples were analyzed using a lab method for surface water. We found that little pollen is airborne over the Indian Ocean in spring, but airborne pollen types and concentrations can help to deduce paleomonsoon strength and direction. The conclusions included the following: (1) Pollen in the sediment was transported mainly via ocean currents instead of the early summer or spring wind. (2) Airborne pollen types and concentrations are proportional to the wind speed and inversely proportional to the pollen distance transported and depend on whether the wind is from the land or from the sea. If the wind is from the land, the pollen concentration is proportional to the angle between the wind direction and the coastline. (3) The pollen concentration in the sample collected from a water depth of 30–45 m is higher than in the samples collected from a depth of 5 m. The pollen concentration and salinity are higher in the equatorial area than in the Northern Hemisphere.

Keywords Northeast Indian Ocean · Airborne pollen · Surface water pollen · Land area

Introduction

Seabed sediments in the northeastern part of the Indian Ocean retain comprehensive information on typical tropical oceans

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and ancient marine environments about the evolution of the South Asian monsoon. The pollen is from terrestrial vegetation, and the occurrence of pollen in marine sediments reflects the vegetation ecology and climatic conditions in the adjacent land to a certain degree.

Ascertaining the pollen transport mechanism is the basis for a correct interpretation of the pollen data from ancient environments. For pollen studies in marine sediments, this issue is more important because the factors controlling pollen distribution in marine sediments are more complex, such as ocean currents, atmospheric circulation, sediment type, large seabed topography, and microlandforms, as well as the mechanisms by which pollen grains sink in the water column onto surface sediments.

In the western Pacific and the South China Sea, research on pollen in marine surface sediments has been gradually carried out in recent years, but similar studies are lacking in the northeastern part of the Indian Ocean. In previous studies, conclusions about pollen analysis in the sediment piston cores still lack modern pollen processes as a reference in the Indian Ocean (Prabhu et al. 2004; Ivory and Lézine 2009), and comparative information is still lacking from modern experiments about the mechanisms of pollen transport from the land to the ocean. Thus, it is difficult to demonstrate that pollen grains

stored in marine sediments can represent the vegetation on adjacent lands. Studying the modern dissemination of pollen in the northeastern Indian Ocean is useful for revealing the characteristic distribution of pollen under a variety of dynamic scenarios in the study area and to reveal the ancient terrestrial vegetation succession in the surrounding area. Some researchers have studied the pollen spread in the air above the major water bodies of the world (Calleja et al. 1993; Dai and Weng 2010; Luo et al. 2015). They collected air pollen samples using the shipboard filter off the western coast of Africa, the western Pacific Ocean, and the South China Sea, respectively, and found that the total pollen concentration and flux depended on the season, pollen type, distance from the pollen source, and wind direction and speed. Some researchers have previously tried to trace spore or pollen movements backwards (Franzen et al. 1994; Hjelmroos and Franzen 1994; Gajewski 1995; Campbell et al. 1999; Bourgeois et al. 2001; Hicks and Isaksson 2006; Rousseau et al. 2008), and back trajectory analysis has been used in recent studies to identify the source of the pollen (Rousseau et al. 2008).

Rivers act a pivotal part in spreading pollen grains to coastal areas (Groot 1971; Heusser and Balsam 1977; Heusser 1988); for example, the concentrations of pollen are higher in sediments collected near river estuaries (Wang and Wang 1987; Bengo 1997; Beaudouin et al. 2007). Changes in wind strength/direction and vegetation patterns (Hooghiemstra et al. 1987; Mudie and McCarthy 1994; Dupont and Wyputta 2003; Vincent Montade et al. 2011), ocean circulation patterns, and fluvial discharge (Chmura and Liu 1990; Vincent Montade et al. 2011) have also been mentioned as important factors in pollen dispersal. The northeast Indian Ocean was selected as the study area. Thirty-six airborne samples along with 26 surface water samples were collected for pollen analysis for the following aims:

1. To reveal the distribution characteristic of modern pollen
2. To explore the main mechanism of modern marine pollen dissemination processes (Fig. 1)
3. To establish a reference for the reconstruction of paleoclimates and even to discover the signal links between marine and terrestrial environments

Materials and methods

Submarine topography

The main topographical characteristics of the northeastern Indian Ocean are the countless volcanic guyots, submerged seamounts, and two subaerial islands. The northeastern Indian Ocean is separated into all types of physiographic divisions

(Supplementary Fig. 1) comprising the Northwest Shelf; the Wombat and Exmouth plateaus; the Cuvier, Argo, and Gascoyne abyssal plains; and the Platypus Spur (Taneja et al. 2015).

The largest area of submarine fans is located in the Indian Ocean (Supplementary Fig. 1), including the two largest submarine fans in the world, the Indus and Bengal fans (Curry et al. 2002; Covault 2011). The largest area of slope terraces and rift valleys is also in the Indian Ocean (IHO 2008; Harris et al. 2014). The Ninety East Ridge is a linear structure on the Indian Ocean floor named for its near-parallel strike along the 90th meridian at the center of the Eastern Hemisphere. It is approximately 5000 km in length and can be traced topographically from the Bay of Bengal southward toward the Southeast Indian Ridge. The ridge extends between latitudes 33° S and 17° N and has an average width of 200 km (Ramana et al. 2000). The ridge divides the Indian Ocean into the West and East Indian Ocean (Stow 2006).

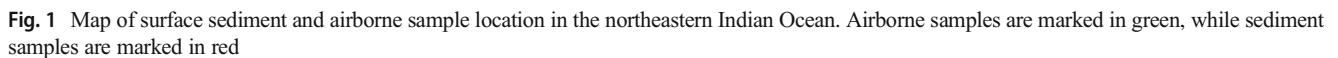
Atmospheric circulation and climate

The northeastern part of the Indian Ocean has a monsoon climate. In summer (May to October), a strong southwest monsoon flows from the Indian Ocean to the Asian continent carrying pollen and spores from the African continent to the northeastern part of the Indian Ocean. In winter (October to April), a north and northeast monsoon flows from the Asian continent to the Indian Ocean carrying abundant tropical and subtropical pollen and spores from southeastern and southern Asia to the northeastern Indian Ocean (Supplementary Fig. 2).

The basin-wide surface wind field is dominated by an alternation between the winter (Supplementary Fig. 2a) and summer monsoons (Supplementary Fig. 2c) (Hastenrath 2007). In winter, the flow from the north recurves near the equator to meet the South Indian Ocean trade winds, whereas in summer, the southern trade winds recurve near the equator to flow into South Asia. During the short transition between the monsoons (Supplementary Fig. 2b and d), strong westerlies occur in the Indian Ocean equatorial zone (Hastenrath 2007).

Oceanic circulation

A complex system of surface currents in the eastern Indian Ocean (Supplementary Fig. 3) moves according to the monsoons and exhibits an obvious seasonality (Gordon and Susanto 1999). From December to March (NW monsoon), the South Java Current (SJC) originating in the Equatorial Counter Current (ECC) flows southeast to meet the Leeuwin Current (LC) (Tomczak and Godfrey 1994). There is a high volume of runoff from Sumatra and Java because of high precipitation during this season. The establishment of an active upwelling system off Java and southwest Sumatra is caused by the prevailing wind direction during the SE



Vegetation

of the Tropic of Cancer. Subtropical forests are distributed in both the eastern and western Himalayas. Temperate broad-leaved forests are distributed in the eastern Himalayas between 1500 and 3000 m elevation and in the Nilgiris in the upper reaches of the Western Ghats (Supplementary Fig. 4). Scrub/shrub areas and small saplings and trees are distributed in northern India, areas of southern India, and the central highlands. Grasslands are both primary and secondary formations occurring in the plains, in abandoned shifting cultivation lands, along with the slopes in the Himalayas and along the coasts of western India (Roy et al. 2015) (Supplementary Fig. 4). Mangroves are found along the western and eastern Indian coasts at river estuaries (Roy et al. 2015). The vegetation on Sri Lanka consists of tropical rainforest in the

southwest lowlands, tropical mountain rain forest at an altitude of 1000–1800 m, and tropical forest at higher altitudes. The most forest is arid monsoon forest, with a small area of tropical rainforest. The major vegetation type in the dry zone of Sri Lanka is a dry semi-evergreen forest. The most common species of forest plants are *Tectona grandis*.

Tropical rain forests in Southeast Asia are mainly distributed in the lowlands near the equator (normally below 600 to 1000 m). Most rain forests are located in Sumatra, Sulawesi, Irian Jaya, and the islands off the Malayan Peninsula. In the palm family, the genus *Calamus* is the most widely distributed. Of the rain forest trees, the Dipterocarpaceae is the characteristic family (Supplementary Fig. 4) (Yan 1984). Monsoon forests are widely distributed in Indochina north of the equator, as well as on some islands south of the equator, such as East Java and the Lesser Sunda islands. *Tectona grandis* (family Verbenaceae), Dipterocarpaceae, Bamboo (family Poaceae) are the representative species in various types of monsoon forests in Southeast Asia. Mountain monsoon forest is mainly distributed at an altitude of 1000–2600 m. *Pinus merkuisi* often grows among species of

Dipterocarpaceae, while *P. insularis* often grows among *Quercus* or *Castanea* (Supplementary Fig. 4) (Yan 1984). Both sides of the equator in Southeast Asia have important distributions of eastern mangrove forests (Yan 1984).

Airborne pollen sampling

In the present study, a total of 36 airborne pollen samples were collected in the northeastern Indian Ocean. We collected 8 airborne pollen samples from April to May in 2010 (Table 1), 16 airborne pollen samples from March to April in 2012 (Table 2), and 12 airborne pollen samples from March to April in 2016 (Table 3, Fig. 1).

Airborne pollen samples were collected during a shared voyage by the National Science Foundation of China (NSFC) in the SCS with a KB-1000 TSP large flow pollen collector manufactured by the Qingdao Jin Shida Electronic Technology Co., Ltd. and placed on the top deck of the vessels *Shiyan 1* and *Shiyan 3*. Each sample was collected for 24–48 h with a much higher rate of instantaneous flow of 1.05 m³/min (Tables 1, 2, and 3) compared to conventional volumetric

Table 1 Pollen characteristics, wind direction and speed, and simulated trajectory 1 day backward of the representative air samples in April to May of 2010

Sample number	Begin time (UTC)	Finish time (UTC)	Finish longitude	Finish latitude	Accumulative total runoff (m ³)	Weather	Pollen assemblage	Wind direction and speed (knots) (0–10 m height)
IND8	April 19 18:00	April 20 18:00	103.04	1.58	1497	Fine	No data	Wind directions are WS; sea surface wind speeds are 5–15 (Fig. 2b,c).
IND9	April 20 18:00	April 21 18:00	99.86	3.93	1554	Short-time shower	<i>Morus</i> , <i>Elytranthe</i> , Rhizophoraceae, Poaceae, Cyperaceae, Davalliaceae, monolete spore, trilete spore	Wind directions are NW; sea surface wind speeds are 5–15 (Fig. 2b,c).
IND10	April 21 18:00	April 22 18:00	97.55	7.18	1449	Fine	<i>Morus</i> , Myrtaceae, <i>Elytranthe</i> , <i>Quercus</i> , Rhizophoraceae, Davalliaceae, Poaceae, Asteraceae, Cyperaceae, monolete spore, Sapindaceae, Taxodiaceae	Wind directions are NW; sea surface wind speeds are 5–15 (Fig. 2b,c).
IND11	April 22 19:00	April 23 19:00	94.20	8.89	1494	Fine	Tree (<i>Morus</i> , Myrtaceae, Verbenaceae, Rhizophoraceae), herb (Poaceae, Melastomataceae, Chenopodiaceae, Asteraceae)	Wind directions are W-N; sea surface wind speeds are 0–5 (Fig. 2b,c).
IND12	April 23 19:00	April 24 19:00	91.26	10.00	1492	Fine	Tree (<i>Morus</i> , Myrtaceae, Verbenaceae, Rhizophoraceae), herb (Poaceae, Melastomataceae, Chenopodiaceae, Asteraceae)	Wind directions are EN; sea surface wind speeds are 5–15 (Fig. 2b,c).
IND13	April 24 19:00	April 25 19:00	90.32	9.98	1501	Fine	Tree (<i>Morus</i> , Myrtaceae, Verbenaceae, Rhizophoraceae), herb (Poaceae, Melastomataceae, Chenopodiaceae, Asteraceae)	Wind directions are ES; sea surface wind speeds are 5–15 (Fig. 2b,c).
IND18	April 29 18:50	April 30 18:50	81.09	10.00	1505	Fine	Tree (<i>Morus</i> , <i>Carpinus</i> , Myrtaceae, Poaceae, <i>Elytranthe</i> , Sapindaceae, Proteaceae), herb (Asteraceae, <i>Artemisia</i>), monolete spore and trilete spore	Wind directions are ES; sea surface wind speeds are 5–15 (Fig. 2b,c).
IND22	May 3 20:20	May 4 20:20	79.85	6.94	1509	Fine	Tree (<i>Morus</i> , <i>Pinus</i> , Taxodiaceae, Sapindaceae), herb (Poaceae), monolete spore	Wind directions are SW; sea surface wind speeds are 5–10 (Fig. 2b,c).

Table 2 Pollen characteristics, wind direction and speed, and simulated trajectory 1 day backward of the representative air samples in March–April 2012

Sample number	Begin day	Finish day	Location (finish)	Accumulative total runoff (m ³)	Pollen assemblage	Wind direction and speed (knots)
12IND11	3.5	3.6	99° 9.954' E, 5° 5.274' S	1510	Trilete spore, <i>Artemisia</i> , <i>Dacrydium</i>	Wind directions are NW-W; sea surface wind speeds are 20–40 (Fig. 3b,c).
12IN-D12	3.6	3.7	97° 44.643' E, 3° 15.987' S	1510	Trilete spore, Cyperaceae, Poaceae, <i>Betula</i> (Fig. 3a)	Wind directions are NW; sea surface wind speeds are 15–25 (Fig. 3b,c).
12IN-D13	3.7	3.8	96° 18.912' E, 0° 46.834' S	1501	Trilete spore, Poaceae, Euphorbiaceae, Rubiaceae, Lamiaceae, <i>Pinus</i> , <i>Betula</i> . pollen concentration is high.	Wind directions are NW; sea surface wind speeds are 5–15 (Fig. 3b,c).
12IN-D14	3.8	3.9	93° 57.684' E, 1° 50.546' N	1489	Polygonaceae, Lamiaceae, <i>Castanopsis</i> (Fig. 3a)	Wind directions are NW; sea surface wind speeds are 5–15 (Fig. 3b,c).
12IN-D15	3.9	3.10	91° 26.238' E, 4° 53.880' N	1484	Trilete spore, Euphorbiaceae, Rubiaceae, <i>Betula</i>	Wind directions are S-SW; sea surface wind speeds are 0–10 (Fig. 3b,c)
12IN-D16	3.10	3.11	89° 29.521' E, 6° 0.111' N	1511	Trilete spore, <i>Artemisia</i> , Cyperaceae, Euphorbiaceae, <i>Betula</i>	Wind directions are EN-E-ES-WN-WS; in the transferring process, sea surface wind speeds are 0–15 (Fig. 3b,c).
12IN-D17	3.11	3.12	88° 29.855' E, 5° 59.714' N	1331	Trilete spore, <i>Castanopsis</i>	Wind directions are E-EN-ES; sea surface wind speeds are 0–10 (Fig. 3b,c).
12IN-D18	3.12	3.13	87° 30.280' E, 5° 59.874' N	853	Trilete spore, Poaceae, <i>Castanopsis</i>	Wind directions are E-S-ES; sea surface wind speeds are 0–15 (Fig. 3b,c).
12IN-D37	4.8	4.9	91° 2.761' E, 0° 1.560' N	1498	Trilete spore, <i>Artemisia</i> , <i>Betula</i> , <i>Alnus</i>	Wind directions are S-W; sea surface wind speeds are 0–10 (Fig. 3b,c).
12IN-D38	4.9	4.1	93° 1.092' E, 0° 1.572' N	1511	Trilete spore, <i>Artemisia</i>	Wind directions are WS; sea surface wind speeds are 5–10 (Fig. 3b,c).
12IN-D39	4.1	4.11	94° 8.582' E, 1° 43.818' N	1457	Trilete spore, <i>Artemisia</i>	Wind directions are WS; sea surface wind speeds are 5–15 (Fig. 3b,c).
12IN-D40	4.11	4.12	94° 26.950' E, 5° 42.106' N	1473	Trilete spore, Poaceae	Wind directions are WS; in the transferring process, sea surface wind speeds are 0–15 (Fig. 3b,c).
12IN-D41	4.12	4.13	98° 16.873' E, 5° 20.607' N	1511	Monolet spore, Poaceae, <i>Pinus</i>	Wind directions are WN; in the transferring process, sea surface wind speeds are 0–10 (Fig. 3b,c).
12IN-D42	4.13	4.14	101° 9.999' E, 2° 42.456' N	1483	Monolet spore, Cyperaceae, Poaceae, Euphorbiaceae, <i>Pinus</i>	Wind directions are EN-ES; sea surface wind speeds are 0–15 (Fig. 3b,c).
12IN-D43	4.14	4.15	104° 27.072' E, 1° 23.218' N	1469	Trilete spore, monolet spore, Poaceae, Euphorbiaceae. The total pollen number is the largest.	Wind directions are ES-WS; sea surface wind speeds are 0–10 (Fig. 3b,c).
12IN-D44	4.15	4.16	106° 25.316' E, 5° 7.275' N	1511	Trilete spore, <i>Artemisia</i>	Wind directions are S-E; sea surface wind speeds are 0–10 (Fig. 3b,c).

techniques, with a longitudinal range of 79° E to 99° E and a latitudinal range of 5° S to 10° N.

The device used for the sampling of airborne pollen uses a brushless motor pump, with long-term continuous work. Air

flow control using high precision sensors and sampling flow are detected automatically, and sampling with constant current is controlled automatically. The total flow and the cumulative time in the process of sampling are recorded automatically.

Table 3 Pollen characteristics, wind direction and speed, and simulated trajectory 1 day backward of the representative air samples in April to May of 2016

Sample number	Begin and finish day	Accumulative total runoff (m ³)	Finish longitude	Finish latitude	Pollen assemblage	Wind direction and speed (knots) (0–10 m height)
EIO02	2016 March 6 to 2016 March 8	3024	110° 48.811' E	7° 21.069' N	<i>Castanopsis</i>	Wind directions are NE; sea surface wind speeds are 5–10 (Fig. 4b,c).
EIO04	2016 March 10 to 2016 March 12	3032.6	107° 30.229' E	4° 53.102' N	Monolete spore, trilete spore, <i>Pinus</i> , <i>Chenopodiaceae</i> , <i>Artemisia</i>	Wind directions are NE; sea surface wind speeds are 5–15 (Fig. 4b,c).
EIO06	2016 March 14 to 2016 March 16	404.2	96° 44.904' E	6° 23.644' S	Monolete spore, trilete spore, <i>Pinus</i> , <i>Proteaceae</i>	Wind directions are WS-WN; sea surface wind speeds are 5–15 (Fig. 4b,c).
EIO07	2016 March 16 to 2016 March 18	437.9	94° 17.816' E	2° 23.644' S	Monolete spore, trilete spore, <i>Poaceae</i> , <i>Quercus</i>	Wind directions are WN; sea surface wind speeds are 0–10 (Fig. 4b,c).
EIO08	2016 March 18 to 2016 March 20	461.9	93° 0.083' E	0° 3.398' S	Trilete spore, <i>Artemisia</i> , <i>Pinus</i>	Wind directions are EN-WN; sea surface wind speeds are 10–25 (Fig. 4b,c).
EIO09	2016 March 20 to 2016 March 22	421.3	91° 55.967' E	2° 0.136' N	Trilete spore	Wind directions are WN-WS; sea surface wind speeds are 5–15 (Fig. 4b,c).
EIO10	2016 March 22 to 2016 March 24	456	90° 34.287' E	4° 30.471' N	Compositae	Wind directions are EN; sea surface wind speeds are 5–20 (Fig. 4b,c).
EIO11	2016 March 24 to 2016 March 26	480	89° 44.611' E	6° 36.949' N	Trilete spore, <i>Chenopodiaceae</i> , <i>Poaceae</i> , <i>Pinus</i> , <i>Castanopsis</i> , <i>Castanea</i> , <i>Salix</i> , <i>Apocynaceae</i> , <i>Moraceae</i>	Wind directions are EN; sea surface wind speeds are 10–15 (Fig. 4b,c).
EIO12	2016 March 26 to 2016 March 28	466	89° 27.081' E	8° 21.043' N	Trilete spore	Wind directions are EN; sea surface wind speeds are 5–10 (Fig. 4b,c).
EIO13	2016 March 28 to 2016 March 30	468.1	90° 43.965' E	4° 9.342' N	Monolete spore, trilete spore, <i>Pinus</i>	Wind directions are EN; sea surface wind speeds are 0–10 (Fig. 4b,c).
EIO14	2016 March 30 to 2016 April 1	535.8	90° 58.647' E	0° 0.904' S	<i>Poaceae</i> , <i>Myrtaceae</i>	Wind directions are EN-WN; sea surface wind speeds are 0–5 (Fig. 4b,c).
EIO15	2016 April 1 to 2016 April 3	547.2	84° 5.587' E	0° 0.023' S	Trilete spore	Wind directions are EN-WN; sea surface wind speeds are 0–10 (Fig. 4b,c).

Waterborne sampling

For this study, 26 samples of surface water were taken in the northeastern Indian Ocean (Fig. 1, Supplementary Table 1). Sixteen samples were taken from 5 May 2014 to 14 May 2014 in the Northern Hemisphere. Ten samples were taken from 20 March 2015 to 2 April 2015 from the equator and the Southern Hemisphere. Surface-water samples (taken at a depth less than 5 m in 2014 and from 30 to 45 m in 2015) were filtered through a fiber membrane with the mesh size of 0.45 µm. Surface-water samples were taken using a submersible pump when the ship was at a seaberthing station (at anchor). From each station, water samples (volumes of 600 and

120–290 l) were taken and filtered over a fiber membrane from the samples collected in 2014 and 2015, respectively.

Laboratory analysis

In the present study, pollen and spores were analyzed, but “pollen” will be used to refer to all pollen and spores in general unless specifically referring to the spores themselves.

The glass fiber filters for atmospheric samples were dissolved in 30 ml HF. Next, we added HCl to remove other impurities. Finally, we added distilled water to the slide mounts. If necessary, the remaining material was filtered

through a 7- μm nylon sieve with an ultrasonic treatment to make the slides clearer.

A 20-ml acetic anhydride liquid mixture (acetic anhydride to the sulfuric acid ratio of 9:1) was added to the 26 surface-water samples to dissolve the fiber membrane used during water sampling. Then, we added acetic anhydride to dissolve the remaining membrane fragments and washed them twice with acetic acid. Finally, the samples were washed in distilled water and mounted on slides with silicone oil (Luo et al. 2016).

The extracted pollen and spores were then prepared for analysis at the Chinese Academy of Sciences (CAS) Key Laboratory of Marginal Sea Geology, SCS Institute of Oceanology, CAS. Pollen and spores were counted under either $\times 400$ or $\times 1000$ magnification. In the surface-water samples, the percentages of individual taxa of pollen and spores and their concentration values (grains/l) were calculated. In the airborne pollen and spores samples, the percentages of individual taxa and their concentration values (grains/ m^3) were calculated. In order to comparing the concentration values of airborne with surface-water samples, 1 grains/l = 1000 grains/ m^3 is used because 1 liter of water equals to 0.001 m^3 of water. Then, we plotted the diagram of percentages of individual taxa of pollen and spores and their concentration values (Figs. 2a, 3a, and 4a) using the C2 software.

Analysis

We compared sea surface wind field observation data from sea level (0 to 10 m) as observed by NASA Quik SCAT satellite equipment (<http://manati.star.nesdis.noaa.gov/datasets/ASCATData.php>) combined with an air particle transfer trajectory HYSPLIT_4 model (http://www.arl.noaa.gov/HYSPLIT_data2arl.php, Draxler and Hess 1998) to infer pollen transmission paths to analyze the relationship between the air movement and pollen spread.

We used Ocean Data View (ODV) to know the water temperature and salinity of the study area, which is a software package for the interactive exploration, analysis, and visualization of oceanographic and other georeferenced profiles, time-series, trajectory or sequence data.

Results

Characteristics of airborne pollen in the northeastern Indian Ocean

The pollen and spore spectra are complex. Twenty pollen and spore taxa were identified. Gymnosperm pollen included *Pinus* spp., *Dacrydium* spp., and *Taxodiaceae*. Angiosperm tree pollen included *Salix* spp., evergreen *Quercus* spp., *Castanopsis* spp., *Castanea* spp., *Ulmus* spp., *Betula* spp., *Myrica* spp., *Oleaceae*, *Euphorbia* spp., *Liquidambar*,

Morus spp. *Sapindaceae*, and *Cycadaceae*. Herbaceous pollen comprised the *Poaceae*, *Fabaceae*, *Cyperaceae*, *Asteraceae*, *Chenopodiaceae*, *Artemisia* spp., *Gentianaceae*, *Euphorbiaceae*, *Labiatae*, and *Lamiaceae* (Figs. 2, 3, and 4).

The air pollen analysis for the 2012 eastern Indian Ocean samples showed that pollen concentration (0–0.02 grains/ m^3) was generally low and the pollen types were much fewer compared with the airborne pollen concentration from 2010 (0–0.16 grains/ m^3).

Analysis of atmospheric wind field and dissemination of pollen

The trajectory figures revealed three navigation passages from different years. We then drew the wind-field map according to the dates of the subpassage. The green line represents the trajectory at 50 m altitude, the blue line at 500 m, and the red line at 3000 m. Pollen was mainly transported by the wind at 50 and 500 m altitude. In a previous study in the South China Sea, Luo et al. (2015) found that the wind at 3000-m height can carry minimal pollen from the nearby islands. The lowest part of the troposphere, where friction with the Earth's surface influences air flow, is the planetary boundary layer. This layer is typically a few hundred meters to 2 km (1.2 mi) deep depending on the landform and time of day (D). Because the content of water vapor and dust is more abundant in this layer, the low clouds, fog, dust, and so on appear frequently in this layer. Pollen belongs to dust, so it is mainly located in this layer. The middle layer (2–6 km) is influenced by the Earth's surface much less than the friction layer, and there is little dust (including pollen) in it.

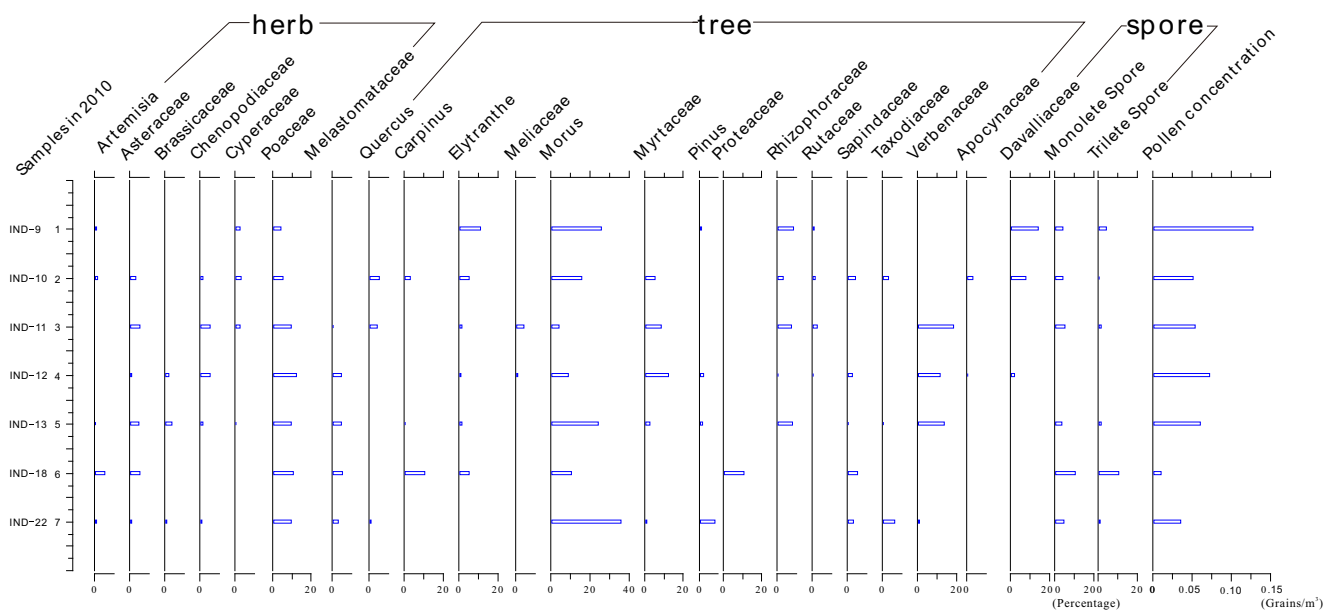
Navigation passage from April to May of 2010

Seven air pollen samples were collected from the eastern Indian Ocean in April 2010 (Fig. 2a). A wide variety of pollen types were found (24 types). The highest amounts of pollen were found in areas IND9 and IND12, and the lowest was in IND18.

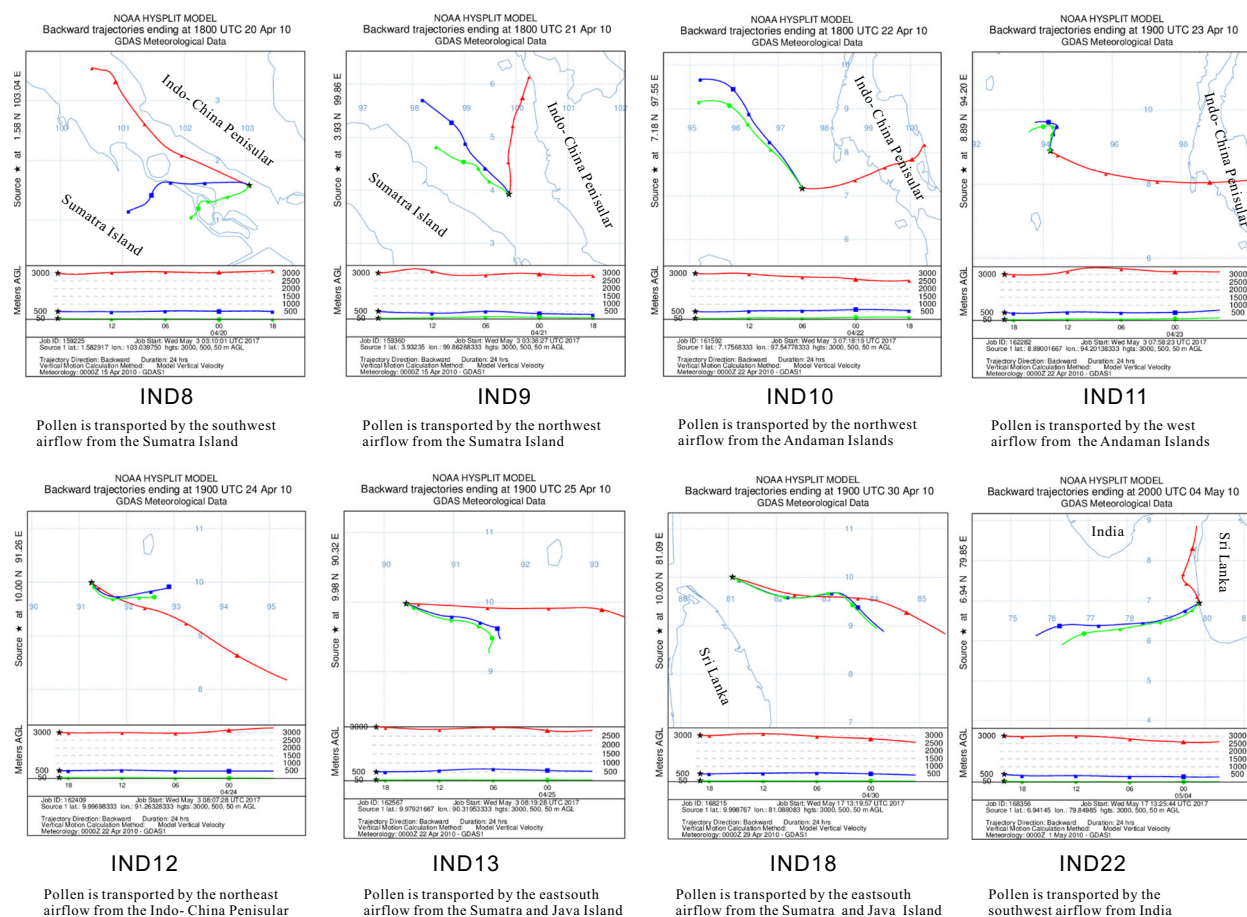
We analyzed the atmospheric wind field and dissemination of pollen from a representative navigation passage from April to May in 2010 (Fig. 2; Table 1).

Over 24 h, ending at 18:00 (Universal Time Coordinated, UTC) on April 21, 2010, the research vessel was mainly influenced by the northwest (50 and 500 m height) and north (3000 m height) airflows. The pollen assemblages were mainly from trees, including *Morus* (from Indonesia, tropical mountain area; *Elytranthe*, *Rhizophoraceae*), herbs (*Poaceae*, *Cyperaceae*), and spores (*Davalliaceae*, monolete spore, trilete spore). The pollen concentration is high with a value of 0.13 grains/ m^3 . The pollen and spore in sample IND9 were mainly from the north part of Sumatra (sample IND9, Fig. 2a–c).

Over 24 h, ending at 19:00 (UTC) on April 24, 2010, the research vessel was mainly influenced by the northeast airflow



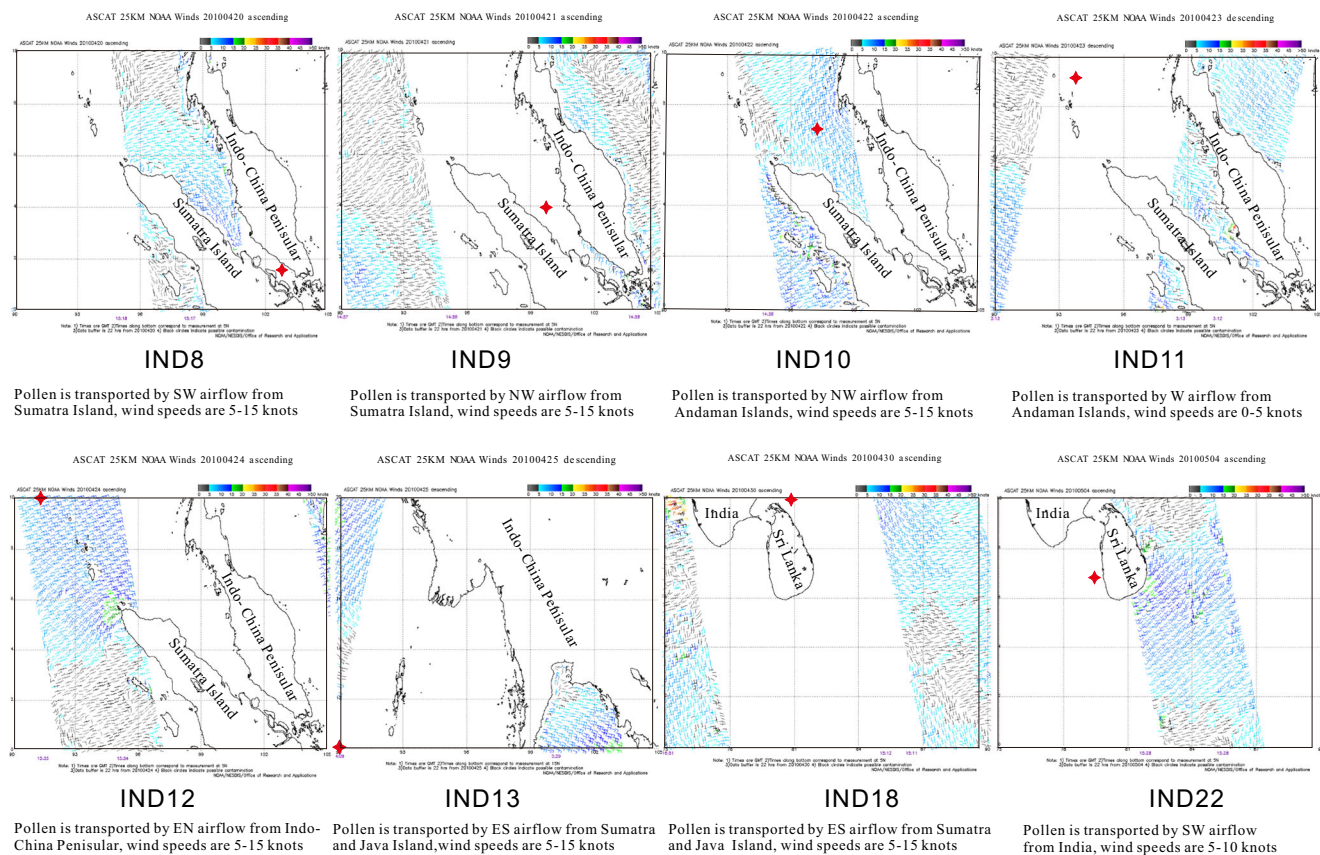
a



b

Fig. 2 **a** Air pollen analysis for samples taken from the northeastern Indian Ocean and the South China Sea from April 2010. **b** The simulated trajectory of airborne pollen for 24 h backward at different altitudes in the sampling areas in April 2010. The green line represents the trajectory at 50 m altitude, the blue line represents the trajectory at

500 m, and the red line represents the trajectory at 3000 m. **c** Wind field (10×15) indicates the wind direction and speed (knots) (0–10 m height). A *blank* indicates an area not scanned by satellite. An *asterisk* indicates the starting site of the air sampling locations. For further information, please see <https://windfarm/manati.orbit.nesdis.noaa.gov>



C

Fig. 2 continued.

(50 and 500 m height) and southeast airflow from a 3000-m height. The pollen concentration is high with a value of 0.075 grains/m^3 . The pollen and spore in sample IND12 were mainly from Indochina Peninsula (sample IND12, Fig. 2).

Over 24 h, ending at 19:00 (UTC) on April 25, 2010, the research vessel was mainly influenced by the southeast airflow. The low wind speed meant that the pollen and spore in sample IND13 were mainly from nearby Sumatra and Java Islands (sample IND13, Fig. 2). The pollen concentration is still high with a value of 0.06 grains/m^3 . The pollen assemblages in samples IND11, IND12, and IND13 were mainly from trees (*Morus*, Myrtaceae, Verbenaceae, and Rhizophoraceae) and herbs (Poaceae, Melastomataceae, Chenopodiaceae, and Asteraceae).

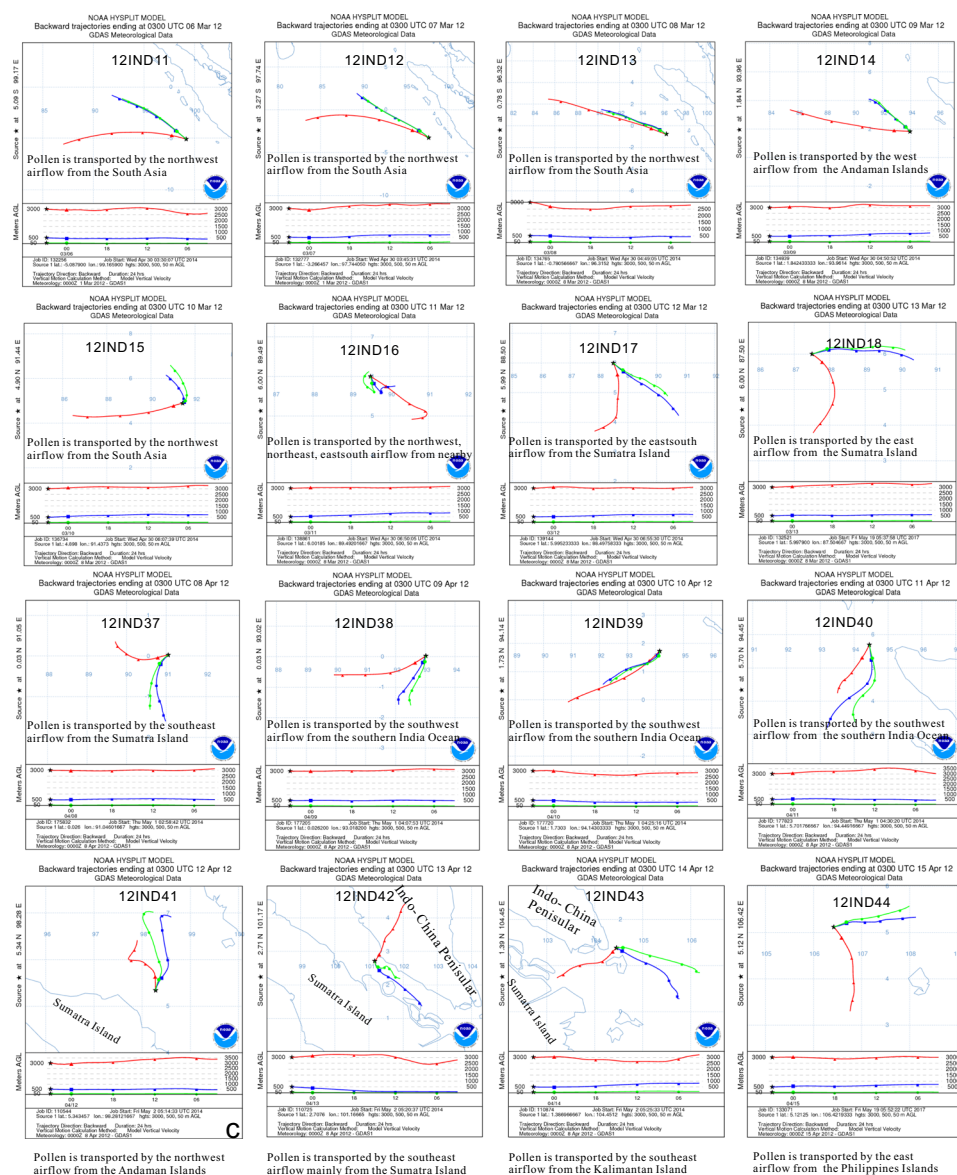
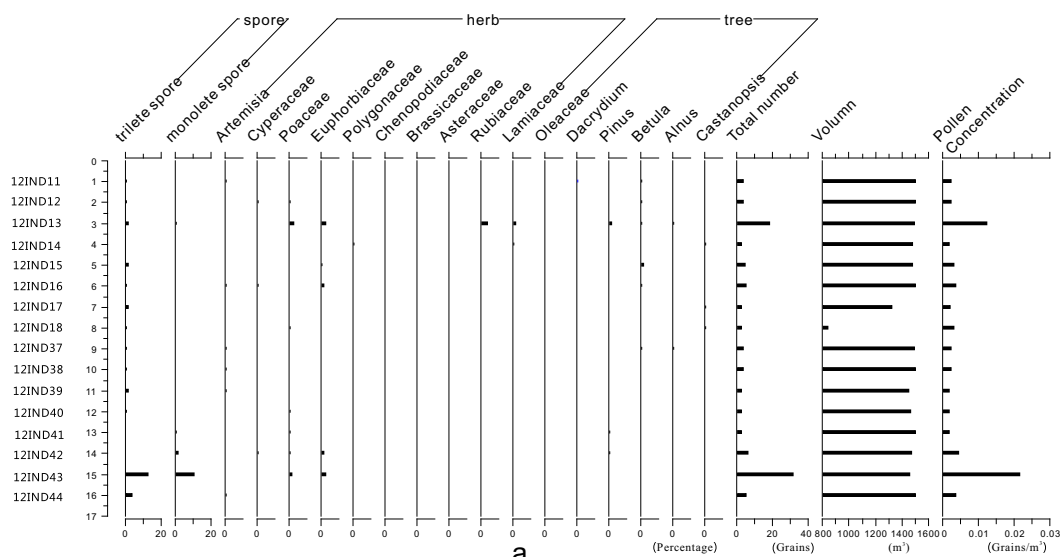
Over 24 h, ending at 18:50 (UTC) on April 30, 2010, the research vessel was mainly influenced by the southeast airflow. The pollen assemblages were mainly from trees (*Morus*, *Carpinus*, Myrtaceae, Poaceae, *Elytranthe*, Sapindaceae, and Proteaceae), herbs (Asteraceae and *Artemisia*), and monolet and trilete spores. The high wind speed meant that the pollen and spores in sample IND18 (located near the island of Sri Lanka) were mainly from distant Sumatra and Java (sample IND18, Fig. 2). The pollen concentration was thus very low with a value of 0.01 grains/m^3 .

For 24 h, ending at 20:20 (UTC) on May 4, 2010, the research vessel was mainly influenced by the southwest airflow. The pollen assemblages were mainly from trees (*Morus*, *Pinus*, Taxodiaceae, and Sapindaceae), herbs (Poaceae), and monolet spores. The pollen types were fewer, and the pollen concentration was not high, with a value of 0.035 grains/m^3 . The low wind speed meant that the pollen and spores in sample IND22 were mainly from nearby Sri Lanka (sample IND22, Fig. 2). The percentage of *Pinus* pollen is the highest; thus, it can be deduced that the *Pinus* pollen is from Sri Lanka.

Navigation passage from March to April in 2012

Sixteen air pollen samples were collected from the eastern Indian Ocean from March to April 2012. From the pollen analyses, samples 12IND13 and 12IND43 in the northeastern Indian Ocean had the most abundant air pollen grains (Fig. 3a). We analyzed the atmospheric wind field and dissemination of pollen from a representative navigation passage from March to April 2012 (Fig. 3; Table 2).

For 24 h, ending at 3:00 (UTC) on March 6 and March 7, 2012, respectively, the research vessel was mainly influenced by the northwest airflow. The pollen assemblages were mainly from trilete spores, *Artemisia*, Cyperaceae, Poaceae,



b

Fig. 3 **a** Air pollen analysis for samples collected from the eastern Indian Ocean from March to April 2012. **b** The simulated trajectory of airborne pollen for 24 h backward at different altitudes in the sampling areas in March 2012. The green line represents the trajectory at 50 m altitude, the blue line represents the trajectory at 500 m, and the red line represents the trajectory at 3000 m. For further air movement trajectory information, please see http://www.arl.noaa.gov/HYSPLIT_data2arl.php (b). **c** Wind field (20×30) indicates the wind direction and speed (knots) (0–10 m height). A blank indicates an area not scanned by satellite. An asterisk indicates the starting site of the air sampling locations. For further information, please see <https://windfarm.manati.orbit.nesdis.noaa.gov>

Dacrydium, and *Betula*. Even the wind speeds (15–40 knots) are very high, but the pollen and spores in samples 12IND11 and 12IND12 were mainly from far away, the island of Sri Lanka (Fig. 3). Thus, the pollen concentrations are low, with both values of 0.003 grains/m^3 .

For 24 h, ending at 3:00 (UTC) March 7 and March 8, 2012, the research vessel was mainly influenced by the north-

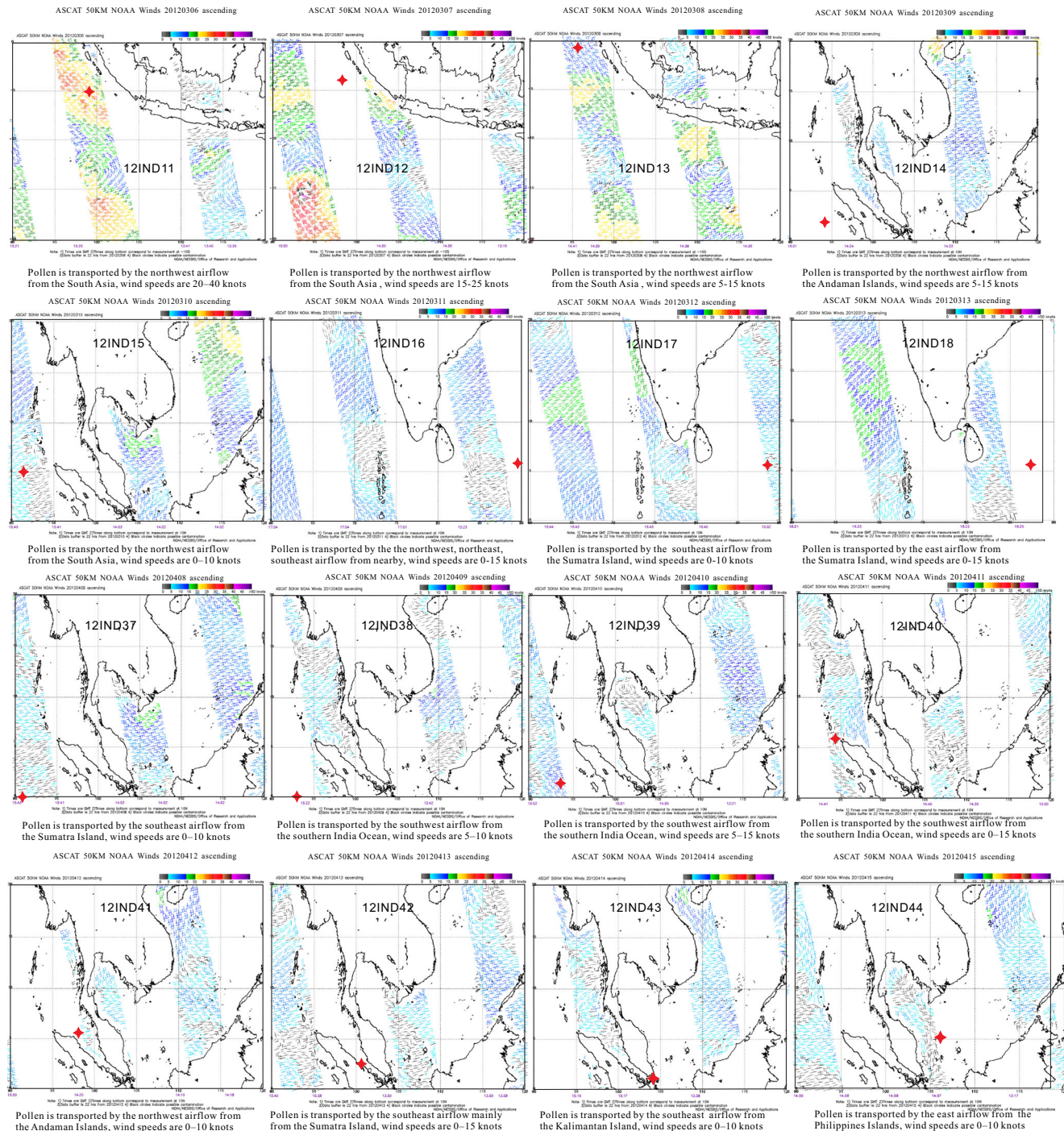
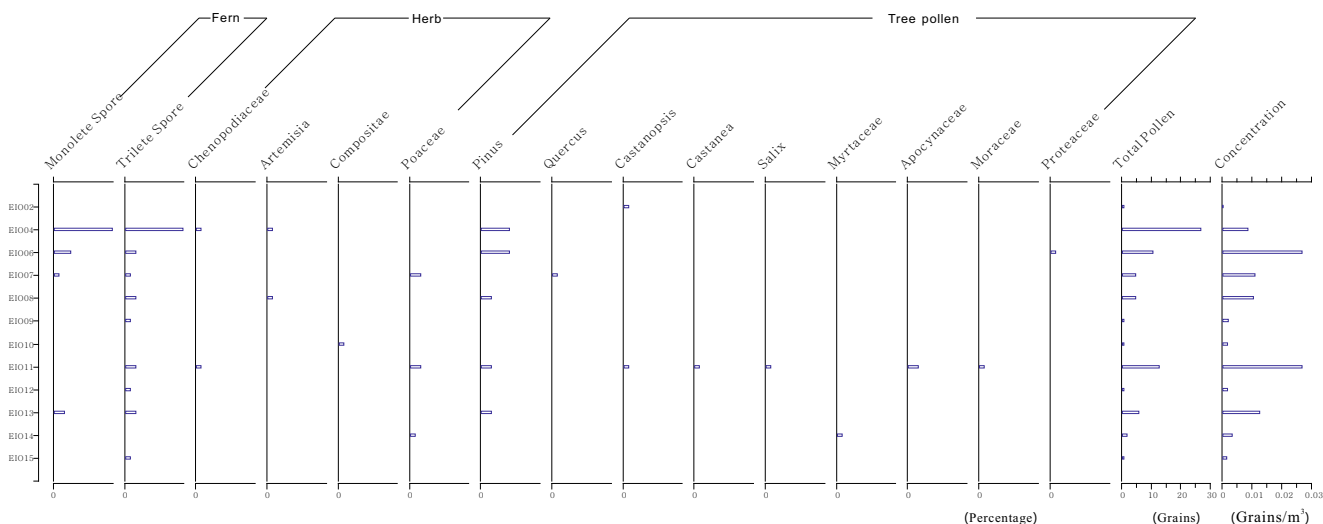
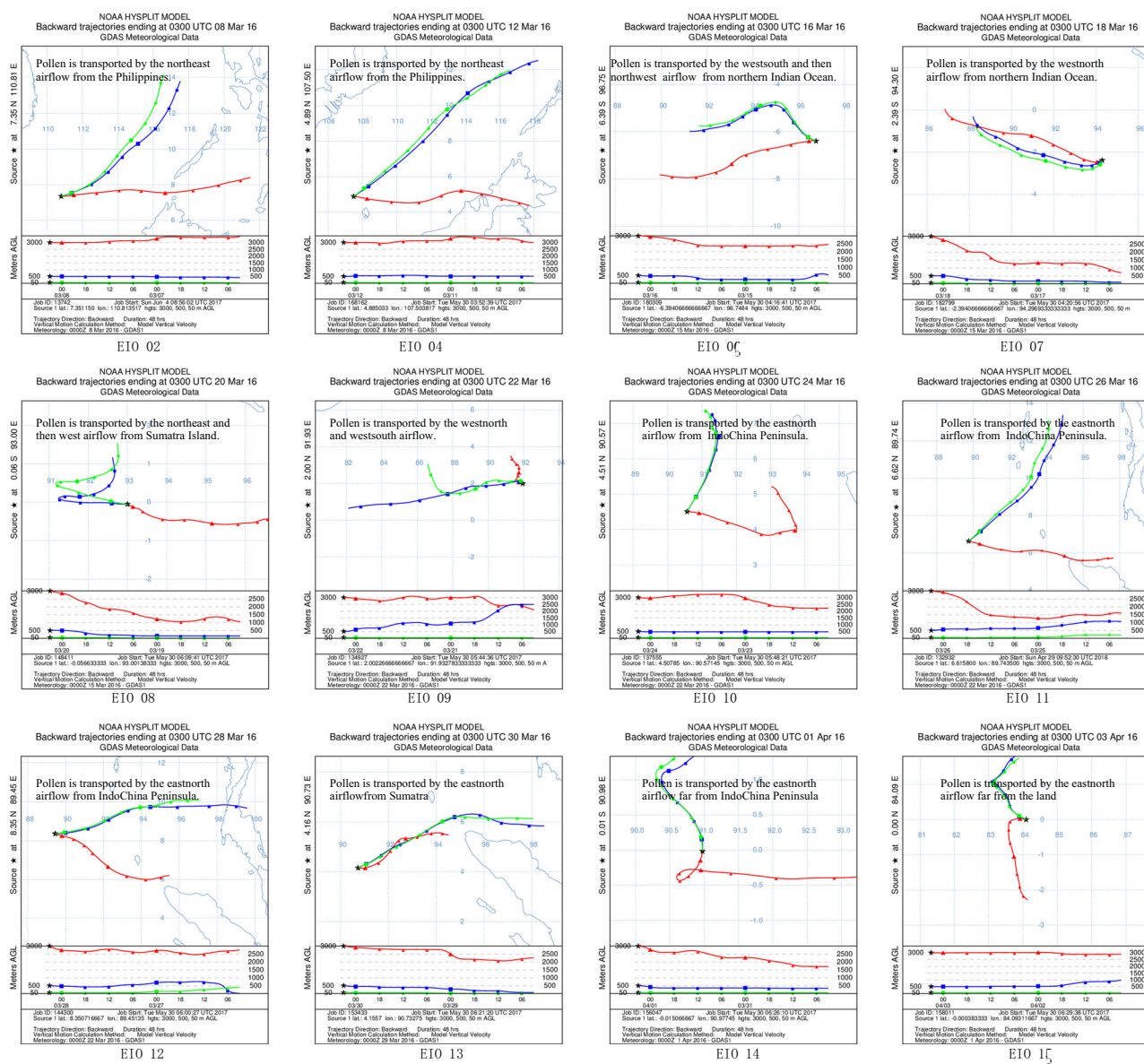


Fig. 3 continued.

c



a



b

Fig. 4 **a** Air pollen analysis for samples collected from the eastern Indian Ocean from March to April 2016. **b** The simulated trajectory of airborne pollen for 24 h backward at different altitudes in the sampling areas in March to April 2016. The green line represents the trajectory at 50 m altitude, the blue line represents the trajectory at 500 m, and the red line represents the trajectory at 3000 m. For further air movement trajectory information, please see http://www.arl.noaa.gov/HYSPLIT_data2arl.php (b). **c** Wind field (20×30) indicates the wind direction and speed (knots) (0–10 m height). A blank indicates an area not scanned by satellite. An asterisk indicates the starting site of the air sampling locations. For further information, please see <https://windfarm/manati.orbit.nesdis.noaa.gov>

west airflow. The pollen assemblages were mainly of variable types, including trilete spores, Poaceae, Euphorbiaceae, Rubiaceae, Lamiaceae, *Pinus*, and *Betula*. From the figures of the 24-h backward trajectory at different heights for the 2012 eastern Indian Ocean samples, the 500- and 50-m altitudes show that the pollen mainly originated in India and Sri Lanka (Fig. 3). The pollen concentration is high, with a value of 0.013 grains/m^3 . The high wind speed (5–15 knots) meant that the pollen and spores in sample 12IND13 were abundant even though they are from far away (Fig. 3).

For 24 h, ending at 3:00 (UTC) on April 8, April 9, April 10, and April 11, 2012, the research vessel was mainly influenced by the south and southwest airflows (50 and 500 m height). The pollen assemblages were mainly from trilete spores, *Artemisia*, Poaceae, *Betula*, and *Alnus*. The pollen concentrations are low, with a value of $0.002\text{--}0.003 \text{ grains/m}^3$. The very low wind speed (0–15 knots) meant that the pollen and spores in samples 12IND37, 12IND38, 12IND39, and 12IND40 were mainly from Sri Lanka (Fig. 3).

For 24 h, ending at 3:00 (UTC) on April 12 and April 13, 2012, the research vessel was mainly influenced by northwest and southeast airflows, respectively. Pollen assemblages were mainly monolete spores, Cyperaceae, Poaceae, Euphorbiaceae, and *Pinus*. The pollen concentrations were low, with values of 0.002 and 0.005 grains/m^3 , respectively. The low wind speed (0–15 knots) meant that the pollen and spores in samples 12IND41 and 12IND42 could not travel far and were mainly from the nearby Indochina Peninsula and Sumatra, respectively (samples 12IND41 and 12IND42, Fig. 3).

For 24 h, ending at 3:00 (UTC) on April 14, 2012, the research vessel was mainly influenced by the southeast

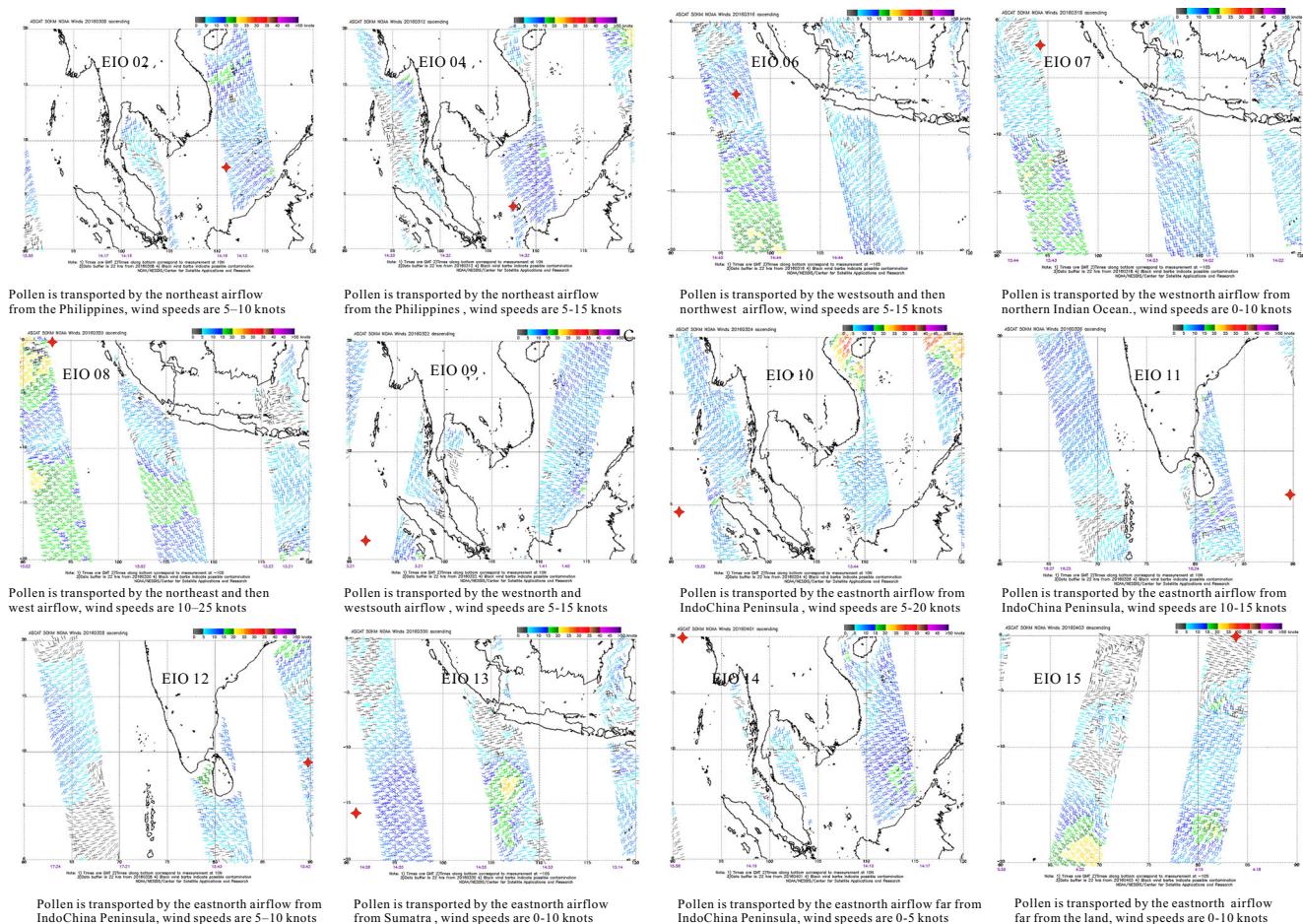


Fig. 4 continued.

airflow (50 and 500 m altitudes). The pollen assemblages were mainly from trilete spores, monolete spores, Poaceae, and Euphorbiaceae. The low wind speed (0–10 knots) meant that the pollen and spores in sample 12IND43 were mainly from nearby Kalimantan Island (sample 12IND43, Fig. 3). This might be the reason that the pollen types are variable and pollen concentration is the highest in sample 12IND43 (0.022 grains/m³).

Navigation passage from March to April in 2016

Twelve air pollen samples were collected from the eastern Indian Ocean from March to April in 2016. From the pollen analyses, in the northeastern Indian Ocean, samples EIO04, EIO06, EIO07, EIO08, EIO11, and EIO13 had high air pollen concentrations (Fig. 4a) (0.01–0.028 grains/m³). We analyzed the atmospheric wind field and dissemination of pollen from a representative navigation passage from March to April 2016 (Fig. 4, Table 3).

For 24 h, ending at 3:00 (UTC) on March 8 and March 12, 2016, the research vessel was mainly influenced by the northeast airflow. The low wind speed (5–10 knots) meant that the pollen and spores in samples EIO02 and EIO04 were mainly from the Philippines, and pollen grains were much fewer in EIO02 and more in EIO04 (sample EIO02 and EIO04, Fig. 4). The pollen assemblages were mainly monolete and trilete spores, *Pinus*, Chenopodiaceae, and *Artemisia* in sample EIO04.

For 24 h, ending at 3:00 (UTC) on March 16 and March 18, 2016, the research vessel was mainly influenced by the southwest and northwest airflows (50 and 500 m height). The pollen assemblages were mainly trilete and monolete spores and *Pinus*, Poaceae, *Quercus*, and Proteaceae in samples EIO06 and EIO07. The pollen concentrations were high, with values of 0.028 and 0.01 grains/m³, respectively. The high wind speed meant that the pollen and spores in samples EIO06 and EIO07 were mainly from the Andaman and Nicobar islands (samples EIO06 and EIO07, Fig. 4).

For 24 h, ending at 3:00 (UTC) on March 20 and March 22, 2016, respectively, pollen in samples EIO08 and EIO09 was mainly influenced by the northeast airflow and northwest airflow (50 and 500 m height, respectively). The pollen assemblages were mainly from very few types, such as trilete spore, *Artemisia*, and *Pinus*. The pollen concentration is still high (sample EIO08, 0.01 grains/m³), but it is low (0.002 grains/m³) in sample EIO09 (Fig. 4a).

For 24 h, ending at 3:00 (UTC) on March 24 and March 26, 2016, the research vessel was mainly influenced by the northeast airflows (50 and 500 m altitude). The pollen types in sample EIO11 are the most varied, and the pollen was mainly influenced by the northeast airflow. The pollen types include trilete spores, Poaceae,

Chenopodiaceae, *Pinus*, *Castanopsis*, *Castanea*, *Salix*, Apocynaceae, and Moraceae. The total pollen *n* percentage is the highest in sample EIO11, and there is only one pollen type (Asteraceae) with very few pollen grains in sample EIO10 (samples EIO10 and EIO11, Fig. 4a).

For 24 h, ending at 3:00 (UTC) on March 28 and March 30, 2016, the research vessel was mainly influenced by the northeast airflow. Even though the wind speed was low in sample EIO13, the pollen concentration is higher in EIO13 than in EIO12; this might be because the distance from EIO13 to the island is closer compared with EIO12 (sample EIO12, Fig. 4a). The pollen assemblages in samples EIO12 and EIO13 were mainly trilete and monolete spores and *Pinus*.

For 24 h, ending at 3:00 (UTC) on April 1 and April 3, 2016, the research vessel was mainly influenced by the northeast airflow. The pollen assemblages are very few and pollen concentrations are low (values of 0.004 and 0.002 grains/m³, respectively). This might be due to the low wind speed in samples EIO14 and EIO15 and the long distance from land (samples EIO14 and EIO15, Fig. 4a).

Characteristics of surface waterborne pollen in the northeastern Indian Ocean

Pollen grains and spores in the surface water samples are very scarce. The pollen and spores are mainly from ferns, trees, and herbs. Fern spores are mainly from *Microlepia* sp., Polypodiaceae, and *Lygodium* sp. Tree pollen is mainly from *Pinus* sp. (Fig. 5a).

The pollen concentration in the sample collected in 2015 at a depth of 30–45 m is higher than in the samples collected in 2014 at a depth of 5 m (Fig. 5b).

Discussion

Pollen transport mechanism based on airborne pollen results

Airborne pollen percentage was generally very low over the northeastern Indian Ocean in spring and early summer, indicating that it was transported by the ocean circulation or delivered in a season other than spring, because we do not know that it is not higher or lower or the same in comparison to any other season, and this is probably because tropical forest trees mainly rely on insectborne pollination; thus, the role of air in pollen transportation is limited (Fig. 2).

The airborne pollen in the samples collected in 2010 was mainly distributed east of the study area, as seen in the higher total airborne pollen percentage of samples IND9 and IND12. Sample IND9 is located in the Straits of Malacca, and the wind was from the northwest.

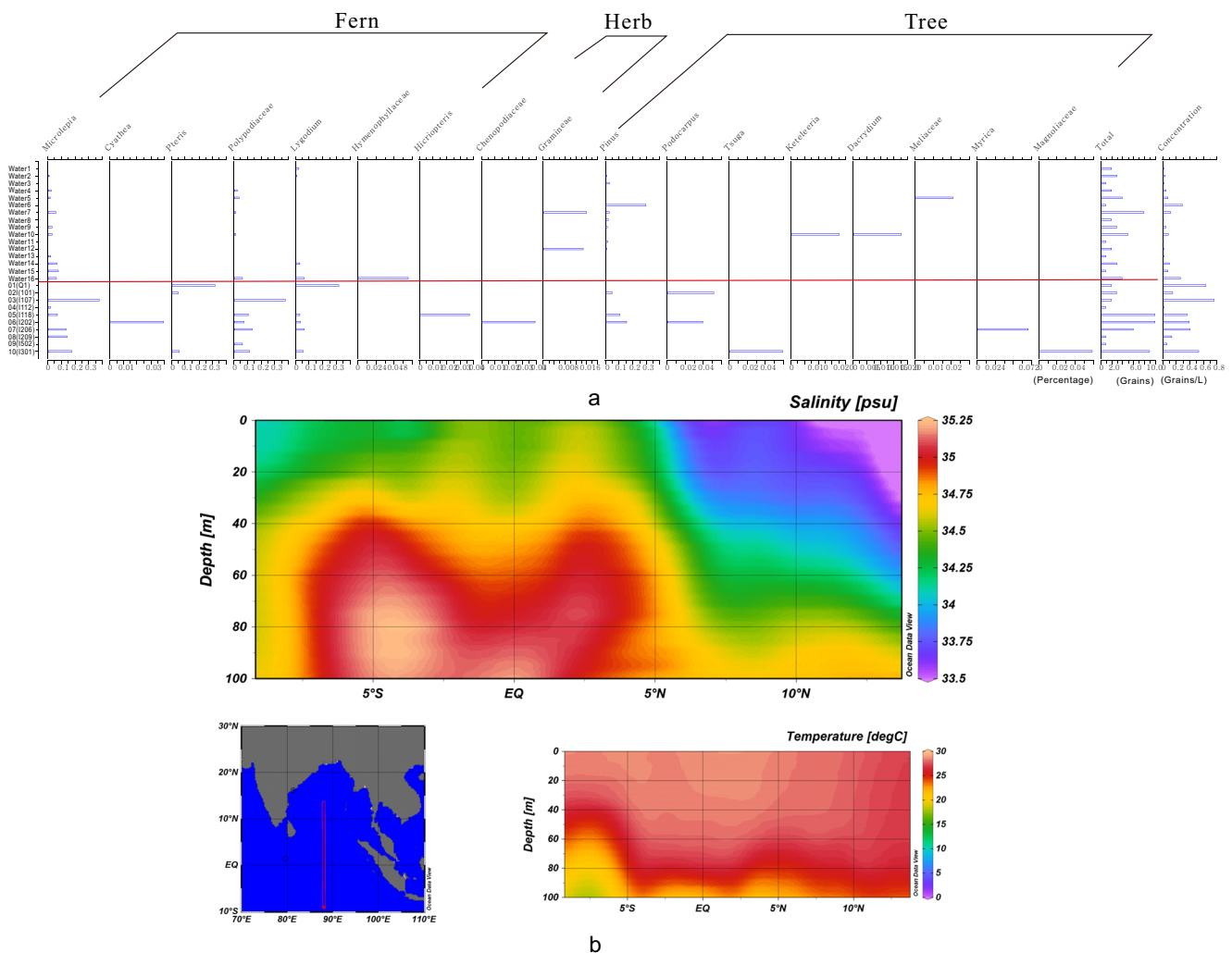


Fig. 5 **a** Pollen concentration of the 26 surface-water samples collected from 2014 to 2015. **b** The water temperature and salinity (with water less than 100 m) in the section at 88° E from 10° S to 15° N, from January to

March from 1955 to 2012 with a revolution of 0.25° based on Ocean Data View (ODV)

Presumably, the pollen in sample IND9 was transported from the southern coastal area of South Asia and adjacent islands. Sample IND12 was located near the island of Sumatra and the Indochina Peninsula, with the wind direction almost perpendicular to the west coastline of the Indochina Peninsula. The total airborne pollen in sample IND18 (located near the island of Sri Lanka) is the lowest because even a high-speed wind from the southeast travels a long distance over the ocean.

From the above descriptions and from samples 12IND11 to 12IND44 collected in March 2012, it could be determined that if the wind speed was high and the wind direction was from nearby land or an island, the pollen types were variable and pollen concentration was high, such as for 12IND13. If the wind speed was low, the pollen types were fewer and the pollen concentration was low, except for sample 12IND43 with pollen from nearby Kalimantan Island. Thus, we can estimate that the pollen concentration is proportional to the

wind speed and is inversely proportional to the distance it was transported, but it also depends on the wind direction and the location of the pollen resource.

In samples EIO02 to EIO15 collected in 2016, the pollen concentration was high in sample EIO08 but low in EIO09 (Fig. 4a). This is because sample EIO08 was influenced by a high-speed (15–30 knots) airflow and the northeast airflow came from Sumatra, while sample EIO09 was influenced by a low-speed (5–10 knots) and northwest airflow coming from the sea. The total pollen percentage is the highest because sample EIO11 was near the Strait of Malacca and the pollen might be from the Indochina Peninsula (sample EIO11, Fig. 4a). There was only one pollen type (an Asteraceae) with very few pollen grains in sample EIO10, which might be because the angle between the wind direction and the coastline was too small (nearly parallel; sample EIO10, Fig. 4a). The pollen grain count was much less in EIO02 and greater in EIO04, probably also because the wind direction had a larger angle

with the coastline in EIO04 than in EIO02. Luo et al. (2015) conducted a palynological analysis based on a different number of air pollen samples for the northern and southern parts of the South China Sea, respectively. They also found that air-borne pollen types and concentrations in the South China Sea have a close relationship with wind direction and distance from the sampling point to the continent. In the present study, the authors specified the function of the angle of the wind direction, and they found that the pollen concentration is proportional to the angle between the wind direction and the coastline. This finding can be used to reconstruct the direction of the paleomonsoon (especially Asia monsoon) based on pollen data in the study area.

The air pollen analysis for the eastern Indian Ocean samples showed that pollen concentration (0–0.02 to 0.16 grains/ m^3) was similar compared with the airborne pollen concentration from the South China Sea (0–0.025 grains/ m^3) (Luo et al. 2015).

Air pollen differences between samples collected from 2010, 2012, and 2016

The air pollen analysis for the 2012 eastern Indian Ocean samples showed that pollen concentration (0–0.02 grains/ m^3) was generally low, and the pollen types were much fewer compared with the airborne pollen concentration from 2010 (0–0.16 grains/ m^3). This is because most of the samples collected in 2010 are from the Malacca Strait near the Andaman and Nicobar islands or in the area of 10° N in the northeastern Indian Ocean (Fig. 1). A lot of pollen and many spores were transported from the Malayan Peninsula and the Andaman and Nicobar islands.

The pollen concentrations in samples collected in 2016 (0–0.03 grains/ m^3) were lower, and the pollen types far fewer than in 2010; however, they are higher than the airborne pollen from 2012. This is because most of the samples collected in April 2010 are from Malacca Strait or the nearby ocean area, with pollen and spores transported from the Malayan Peninsula and Andaman and Nicobar islands. Most of the samples collected in March 2016 are from the west coastal water near Sumatra with a sampling time of 2 days. Most of the samples collected from March to April 2012 are also from the west coastal water near Sumatra, but the sampling time was only 1 day.

The pollen spectra of the 26 surface-water samples in different years

Pollen concentrations (with an average value of 0.025 grains/l) in the water sample collected in 2015 at a depth of 30–45 m (volumes of 120–290 l were taken and filtered over a fiber membrane) are higher than the pollen concentrations (an average of 0.004 grains/l) of the samples collected in 2014 at a

depth of 5 m (600 l was taken and filtered over a fiber membrane). The reason was not clear until now when the following was found:

1. The pollen concentration is positively correlated with water temperature and salinity in water depths greater than 50 m in the study area. For example, at a depth of 30–45 m, the pollen concentration is higher than at 5 m. The salinity became higher and temperature lower as the water became deeper (more than 100 m) in the section at 88° E from 10° S to 15° N, from January to March from 1955 to 2012 with a resolution of 0.25° based on ODV (Fig. 5b).
2. The pollen concentration and salinity are higher in the equatorial area than in the Northern Hemisphere.

The mechanisms of the above two findings are still unclear, and more study is needed to reveal them (Fig. 5b).

Pollen concentrations (with an average value of 0.017 grains/l) in the water sample collected in the northeastern Indian Ocean are lower than the pollen concentrations (with an average value of about 0.08–0.1 grains/l) in the water sample collected in the South China Sea (Luo et al. 2016). The reason might be that the northeastern Indian Ocean is an open ocean while the South China Sea is a margin sea with continent and islands around it and a lot of rivers putting into the SCS.

Conclusions

Little pollen is airborne over the Indian Ocean in the spring, so perhaps it was transported mainly via the ocean circulation instead of on the spring and early summer wind.

We can estimate that the pollen types and concentrations are proportional to the wind speed and inversely proportional to the distance the pollen was transported; pollen types and concentrations also depend on whether the wind is from the land or the sea. If the wind is from the land, the pollen concentration is proportional to the angle between the wind direction and the coastline.

The pollen concentration in the sample collected in 2015 at a depth of 30–45 m is higher than in the samples collected in 2014 at 5 m. Pollen concentration is positively correlated with salinity and negatively correlated with temperature at depths greater than 100 m in the study area. The pollen concentration and salinity are higher in the equatorial area than in the Northern Hemisphere.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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