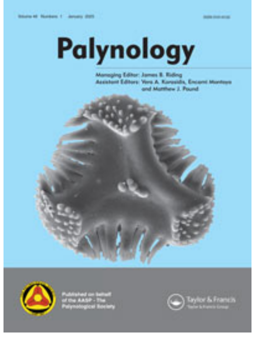

Palynology

ISSN: (Print) (Online) Journal homepage: www.tandfonline.com/journals/tpal20

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To cite this article: Dongmei Cheng, Zhongxin Duan, Qiqi Li, Zetian Liu, Yumei Yan, Luping Zhou & Zhiyong Zhang (01 Dec 2024): Vegetation changes of Lushan, China between 1959 and 2020 based on pollen data, Palynology, DOI: 10.1080/01916122.2024.2428378

To link to this article: https://doi.org/10.1080/01916122.2024.2428378

PALYNOLOGY
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Vegetation changes of Lushan, China between 1959 and 2020 based on pollen data

Dongmei Cheng[a], Zhongxin Duan[a], Qiqi Li[a], Zetian Liu[a], Yumei Yan[a], Luping Zhou[b], and Zhiyong Zhang[a]

[a]Jiangxi Provincial Key Laboratory of Wetland Plant Resources Conservation and Utilization, Lushan Botanical Garden, Jiangxi Province and Chinese Academy of Sciences, Jiujiang, China; [b]Jiangxi Lushan National Nature Reserve, Lushan, China

ABSTRACT

Both climatic change and human activity are currently driving the dynamic of vegetation, which may vary from region to region. On Lushan Mountain, located in eastern China, the subtropical secondary forests during the natural succession endure the pressure from ongoing climate warming on the one hand. They are influenced by anthropogenic disturbance on the other hand for recent decades. Previously, palynological research has discovered that the pollen assemblages from surface soil samples on Lushan reflect the characteristics of local vegetation. Here, we did a comparative study by using pollen analysis to investigate the vegetation changes of Lushan from 1959 to 2020. We compared the composition of pollen assemblages obtained in 1959 with that in 2020 along different altitudes. Further, the biomisation method was employed to discover the changes of different vegetation types, which were reflected by the pollen-based reconstructed biomes. Meanwhile, the temporal beta diversity analysis was used to extract the sites: that experienced significant vegetation shift and the most important taxa change. Results showed that the pollen composition over the past 60 years on Lushan had altered remarkably. The vegetation shifted at all altitudes. The current vegetation pattern of Lushan: evergreen broadleaved forest at low elevation, temperate deciduous broadleaved forest at middle elevation and cool mixed forest at high elevation, is the successional consequence of the past 60 years. The forces driving the vegetation dynamics might be from multiple sources. However, human disturbance seems to play quite an important role during forest succession. Our study is potentially useful both for paleoecological reconstructions and wider understanding of current climate change that are relevant to subtropical forests of Asia.

KEYWORDS
Vegetation succession; pollen spectrum; human disturbance; biomisation; temporal beta diversity

1. Introduction

From polar terrestrial to tropical marine environments, anthropogenic climate change has been frequently recorded in terms of the ecological impacts (Walther et al. 2002; Kelly and Goulden 2008; Lenoir et al. 2008; Chen et al. 2011). A noteworthy example is the montane ecosystem, which is especially sensitive and responding disproportionately to the period of warming (Verlhac et al. 2018; Hagedorn et al. 2019). Plant species in mountain biota shift their distribution ranges under the climatic pressure (Rahbek et al. 2019). This species shift in vertical direction may lead to rapid reorganization in vegetation structure (Thuiller et al. 2006). Further, ecological processes that could be stochastic or deterministic drive the community assembly and diversity maintenance during forest succession (Bruelheide et al. 2011). Besides changing climate, other forces could also drive the community composition, such as all kinds of disturbances whether they are human-induced or natural sources (Dale et al. 2001).

Pollen-vegetation relationship for palynologists provides a way to understand the characteristics of both modern and past vegetation. A large number of studies have proved that modern pollen assemblages in mountainous areas generally reflect the vegetation types in terms of main pollen taxa (e.g. Yu et al. 2001; Herzschuh et al. 2010; Li et al. 2012; Zhang et al. 2014; Fang et al. 2015; Wei and Zhao 2016; Verlhac et al. 2018; Karachurina et al. 2023). On the basis of contemporary pollen-vegetation relationship, the past vegetation could be comprehensively reconstructed relying on palaeovegetation reconstruction techniques (Cruz-Silva et al. 2022). Moreover, the past biodiversity for historical vegetation can be extracted as well with the help of pollen proxy (Odgaard 1999; Matthias et al. 2015; Liang et al. 2019). However, the corresponding pollen-vegetation-diversity relationship is indeed complicated during the practice, and inherent problems or biases might happen for a specific case study (Birks et al. 2016).

Human activities had destroyed original forests and vegetation on Lushan before 1936 (Chen 1936). After at least two decades of vegetation restoration and succession, the secondary forests gradually formed (Zheng 1956). According to the vegetation survey conducted in 1959 (Li 1985), the vertical vegetation belts have already been successfully distinguished along altitudes. This potential natural vegetation (also secondary status) has more or less still endured the

CONTACT Zhiyong Zhang zzyzwx@126.com Jiangxi Provincial Key Laboratory of Wetland Plant Resources Conservation and Utilization, Lushan Botanical Garden, Jiangxi Province and Chinese Academy of Sciences, Jiujiang, China

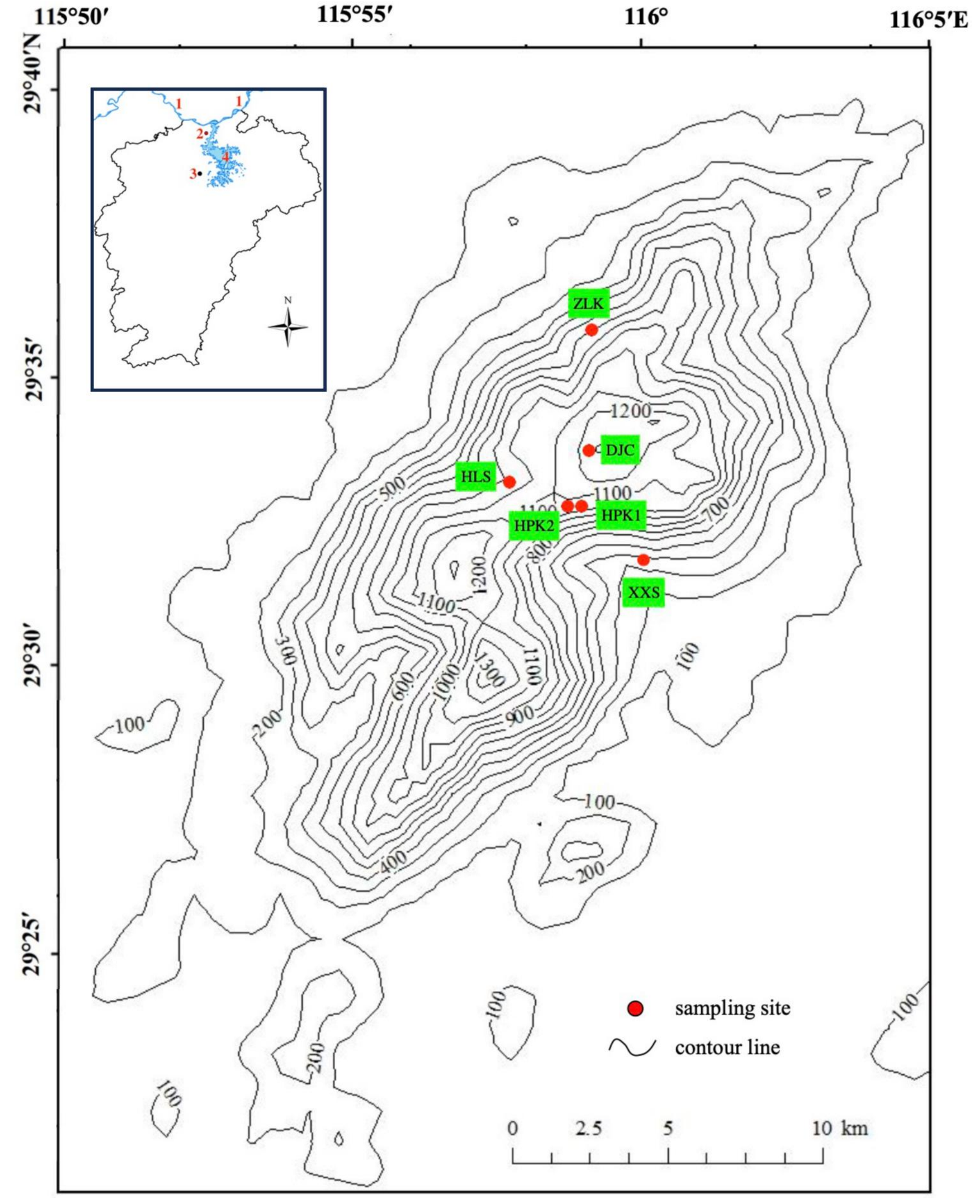

Figure 1. Lushan mountain and sampling sites. Inset is the map of Jiangxi Province. 1. Yangzte River; 2. Lushan; 3. Nanchang; 4. Poyang Lake.

human-induced disturbance from 1936 to 1959, like firewood collecting and grazing. Nevertheless, palynological study has discovered the objective pollen-vegetation relationship (Li 1985), which allows us to know more details on the past vegetation of Lushan for 1950s. Here, we do a comparative study with that of Li (1985) relying on the methods of biome reconstruction and temporal beta diversity analysis. We revisited Li's sampling sites (Li sampled in 1959) and collected surface soil samples in 2020 in order to illustrate the changes of vegetation and plant diversity over the past 60 years on Lushan.

2. Methods and materials

2.1. Physical environment

Lushan is a horst-style block mountain in Jiangxi Province of China, which coexists with Poyang Lake on the east and the middle-lower part of Yangzte River on the north (Figure 1). It covers an area of ca. 300 km^2 with a highest spot called 'Hanyang Peak', having an elevation of 1474 m (Liu and Wang 2010). Literally, Lushan is quite steep. With increasing altitude, the land area is reducing remarkably. For example, land areas from 500 m upward are only 1–3% of the total area for each 100 m interval. The climate of Lushan is mainly controlled by the subtropical monsoon. During 1960–2019, the mean annual temperature has been estimated to increase around 1.2 Celsius degree (Li et al. 2022).

2.2. Sampling sites and pollen data

Six sites were described in the paper of Li (1985), in which surface soil samples had been collected from various vegetation types with different elevations in 1959. Following the detailed description of sampling sites (Li 1985), we revisited those six sites and collected surface soil samples (0–3 cm) in 2020 again. At the same time, we recorded the exact

Table 1. Details of sampling sites on Lushan.

Sites	Longitude (E)	Latitude (N)	Altitude (m)	Vegetation in 1959	Observed vegetation in 2020
XXS	116.003	29.519	400	*Pinus massoniana* forest	Evergreen broadleaved forest with patchy conifer
ZLK	115.986	29.597	600	Evergreen broadleaved forest	Evergreen and deciduous broadleaved mixed forest
HLS	115.962	29.553	900	Evergreen and deciduous broadleaved mixed forest	Evergreen and deciduous broadleaved mixed forest
HPK1	115.983	29.546	1100	Deciduous broadleaved forest	Conifer and broadleaved mixed forest
HPK2	115.979	29.546	1200	*Pinus taiwanensis* forest	Conifer and broadleaved mixed forest
DJC	115.985	29.562	1285	Shrubland and meadow	Conifer and broadleaved mixed forest

The description of vegetation in 1959 is from the record of Li (1985). Observed vegetation in 2020 is based on the field survey in the year of 2020 when taking the samples.

coordinates of sampling sites (see Figure 1; Table 1 for Details of sampling sites). For sites HLS, HPK1 and HPK2 where we think there might be some possible disturbance, we collected three samples and finally took an average of the data. The pollen data for samples in the year of 1959 is listed out in Li's (1985) paper, which allows us to have a chance to do a comparative study on the variation of pollen assemblages between 1959 and 2020. Each 50 g sample was processed by HCl (15%), NaOH (10%) and HF acid in turn. After centrifuging and sieving, the residues were stored by using 50% glycerol. Finally, microscopic slides were made for pollen identification and counting (more than 400 pollen grains per sample). The percentage of each pollen taxon was calculated relative to the sum of all taxa present. We recalculated pollen percentages data of 1959 according to the original pollen count, including taxa both from woody and herb plants.

2.3. Biome reconstruction

The biomisation method based on pollen data is a semi-quantitative approach for vegetation reconstruction (Prentice et al. 1996; Cruz-Silva et al. 2022). A main concept for the method of biomisation is plant functional type (PFT), which links a set of pollen taxa to a specific biome. Theoretically, a biome can be reconstructed if pollen percentage data is available for a sampling site following the comprehensive scheme of taxa-PFT-biome assignment (e.g. Jolly et al. 1998; Yu et al. 1998; Harrison et al. 2001; Pickett et al. 2004; Ni et al. 2014). Currently, there is no general agreement on PFT classification at a global scale (Harrison et al. 2010), and it usually needs modifications for biome reconstruction when considering a continental or regional scale (e.g. Ni et al. 2014; Verlhac et al. 2018; Sun et al. 2020; Zheng et al. 2023). Given this fact, we have to treat the reconstructed biome with some caution. In this paper, we follow three ways of pollen taxa-PFT-biome assignment put forwarded by Zheng et al. (2023), Sun et al. (2020), and Ni et al. (2014) separately, in order to interpret the changes of vegetation types (biome) over the past 60 years (1959–2020) on Lushan. Within these three studies, potential natural vegetation in subtropics is treated in different ways. For instance, Zheng et al. (2023) defined subtropical evergreen broadleaved forest (EBLF) as the most indicative zone biome in subtropics that contains six key PFTs. Sun et al. (2020) admitted three subzone biomes: north subtropical mixed forest (WAMF), middle subtropical broadleaf evergreen forest (MTFO) and south subtropical broadleaf evergreen (STFO). In contrast, Ni et al. (2014) treated the subtropical biomes as two variants, that is, warm–temperate evergreen broad-leaved and mixed forest (WTEM) and warm–temperate evergreen broad-leaved forest (WTEG). These biome definitions more or less overlap, probably because they want to do some compromise when considering both the latitudinal and altitudinal climatic gradients. After all, the subtropics in China occupy quite a vast area with the remarkably diverse vegetation.

Meanwhile, we have noticed that a few assignments of pollen taxa into certain PFTs may not be appropriate in the paper of Sun et al. (2020). For example, the genus of *Cyclocarya* has only one species *Cyclocarya paliurus* in China, which is deciduous in leaf phenology (Fang et al. 2011; Flora of China 2023). Unfortunately, it was assigned into the PFT of subtropical evergreen. Likewise, *Prunus* and *Rhoiptelea* are deciduous rather than evergreen. For the family of Saxifragaceae, many plant species are shrubs and deciduous (Fang et al. 2011; Flora of China 2023), thus it may be also unsuitable to put this taxon into tropical and subtropical evergreen forbs. After careful checking of taxa-PFTs assignment and modification, we do the subsequent biome reconstructions on the basis of our pollen data.

We followed the standard procedure of biomisation method to do biome reconstructions (Prentice et al. 1996; Prentice and Webb 1998) through three different classification systems of PFT-biome introduced by Zheng et al. (2023), Sun et al. (2020), and Ni et al. (2014) separately. To down-weight over-represented taxa, a universal threshold of pollen percent is set, e.g. usually use 0.5% as default value (Williams et al. 2000). However, we also take a balance for considering the under-represented taxa that might be diagnostic for a particular PFT (Cruz-Silva et al. 2022). Thus, five threshold values (0.1%, 0.25%, 0.5%, 0.75% and 1%) in terms of pollen percentage are tried to explore the sensitivity of reconstructed biome switch.

2.4. Temporal beta diversity index

Temporal beta diversity index (TBI) is a statistical method that is designed for analyzing the change of beta diversity during two different survey times (Legendre 2019). It usually involves several sites and can help to identify exceptional sites where the significant differences have taken place. Applications of this method have already been published in many studies related to both terrestrial and aquatic communities (e.g. Legendre and Salvat 2015; Winegardner et al. 2017; Kuczynski et al. 2018; Legendre and Condit 2019). The objective of TBI is to illustrate whether the temporal changes among multiple sites are dominated by species losses (B statistics) or by gains (C statistics), which can be distinctly shown *via* the B-C plot. Here, we employ TBI method to explore the temporal beta diversity changes (during 1959–2020) for different altitudinal sampling sites on Lushan, and to further understand the potential vegetation shifts based on pollen proxy. Because of the resolution of pollen identification, the taxa level (family or genus) is used when computing species gains and losses that are two necessary parts in an ordinary TBI analysis.

After finishing TBI analysis, we also want to know how much the alterations of taxa composition are on Lushan over the past 60 years. Thus, paired t-tests are carried out for all taxa both in 1959 and 2020. Each test is performed with 9999 random permutations of the values and Holm method for p value correction (method details in Legendre and Condit 2019).

TBI calculation and B-C plot are implemented in the TBI () and plot.TBI () functions separately, available in R package adespatial (Dray et al. 2024); And paired t-tests are implemented in the function tpaired.krandtest (), also available in this package.

3. Results

3.1. Variations of major taxa within pollen assemblages

The top ten abundant pollen taxa for each sample site are listed in Figure 2. For the site of XXS with the lowest elevation of 400 m, the major taxa in pollen assemblage were *Pinus*, *Quercus*, *Castanopsis* and *Castanea* in 1959, while the majorities are *Pinus*, Poaceae and *Hamamelidaceae* in 2020. For the site of ZLK with an elevation of 600 m, the major pollen taxa were *Castanopsis*, *Pinus*, *Quercus*, *Cunninghamia*, *Juniperus*, *Castanea* and *Rhododendron* in 1959, while only *Pinus* increases dramatically up to around 80%, also with *Quercus* decrease and *Cryptomeria* increase in 2020. At HLS with a middle elevation of 900 m, *Pinus*, Hamamelidaceae and *Cryptomeria* increase in abundance in the year of 2020 compared to the year of 1959. *Quercus, Castanopsis, Castanea* and *Cunninghamia* decrease during 1959–2020. At the sites of HPK1 and HPK2 with the elevations of 1100 m and 1200 m, the most abundant pollen taxon is *Pinus* both in 1959 and 2020. However, the remaining within the top ten is different. For example, the pollen taxa of *Quercus* occur and *Castanea* and *Platycarya* disappear within the top ten in 2020, compared to 1959 at HPK1. At the site of DJC with the highest elevation of 1285 m, *Pinus* increases distinctively, while *Artemisia* decreases remarkably during 1959–2020. *Quercus* decreases slightly in abundance as well at this period.

3.2. Reconstructed biomes for different sites in 1959 and 2020

The reconstructed biome for the site of XXS most likely changed from DBLF (Temperate deciduous broadleaved forest) in 1959 to EBLF (Subtropical evergreen broadleaved forest) in 2020 (Table 2), which is under the PFT-Biome classification of Zheng et al. (2023). However, there is an exception for the case of 1% threshold where the reconstructed biomes are both DBLF. This biome change cannot be confirmed by the reconstructions *via* PFT-Biome classifications of both Sun et al. (2020) and Ni et al. (2014). For site of ZLK, the reconstructed biome most likely changed from EBLF in 1959 to DBLF in 2020 when using Zheng's PFT-Biome classification, but not for 0.1% reconstruction case. The biome shift of ZLK is also identified from TSFO (Tropical seasonal forest) in 1959 to CLEC (Cold-temperate evergreen conifer forest) in 2020 when using Sun's PFT-Biome classification, except the 0.1% reconstruction case again. For the site of HLS, the reconstructed biomes are EBLF in 1959 and DBLF in 2020 *via* Zheng's PFT-Biome framework. In contrast, the reconstructed biomes either keep the same as WAMF (North subtropical mixed forest) or change from WAMF in 1959 to CLEC (Cold-temperate evergreen conifer forest) in 2020 *via* Sun's PFT-Biome framework. In any threshold cases for XXS, ZLK and HLS, the reconstructed biomes are always WTEM (Warm–temperate evergreen broad-leaved and mixed forest) during this period when using Ni's PFT-Biome classification.

At the site of HPK1, the reconstructed biome is EBLF in 1959, while it is either COMX (Cool mixed forest) or CLMX (Cold mixed forest) in 2020 when Zheng's PFT-Biome framework is used and the threshold is over 0.1% (Table 2). The reconstructed biome is CLEC both in 1959 and 2020 *via* Sun's PFT-Biome framework, though the biome has changed from WTEM to CLDE (Cold deciduous forest) *via* Ni's PFT-Biome classification for pollen threshold value over 0.5%. For site HPK2, the biome changed from EBLF in 1959 to COMX in 2020 under Zheng's PFT-Biome situation, whereas the biome is always either CLEC or WTEM at this period under Sun's and Ni's frameworks. At DJC, the reconstructed biome is DBLF in 1959, while it could be COMX or CLMX in 2020 *via* Zheng's PFT-Biome framework. The reconstructed biome for the site of DJC is always CLEC in any cases under Sun's PFT-Biome situation. However, it is WTEM for most of reconstructed biomes when using Ni's PFT-Biome classification, except for the case of 0.75% and 1% in 2020 (the reconstructed biome is CLDE).

3.3. B-C plot for abundance of pollen taxa

In this overall plot, the green line is below the red line, indicating gains of abundances-per-taxon dominated the changes in the entire Lushan from 1959 to 2020 (Figure 3). Specifically, abundances-per-taxon is gained the most at ZLK and the least at DJC. Sites of HLS, HPK1 and XXS have the intermediate gains of taxa abundances. On the contrary, abundances-per-taxon is lost at HPK2. Changes of taxa abundances in sequence are: ZLK > HLS > HPK1 > XXS > DJC > HPK2.

3.4. Changes in taxa composition from 1959 to 2020

The paired t-tests computed separately for overall taxa showed that one-third taxa had the increases in relative abundances

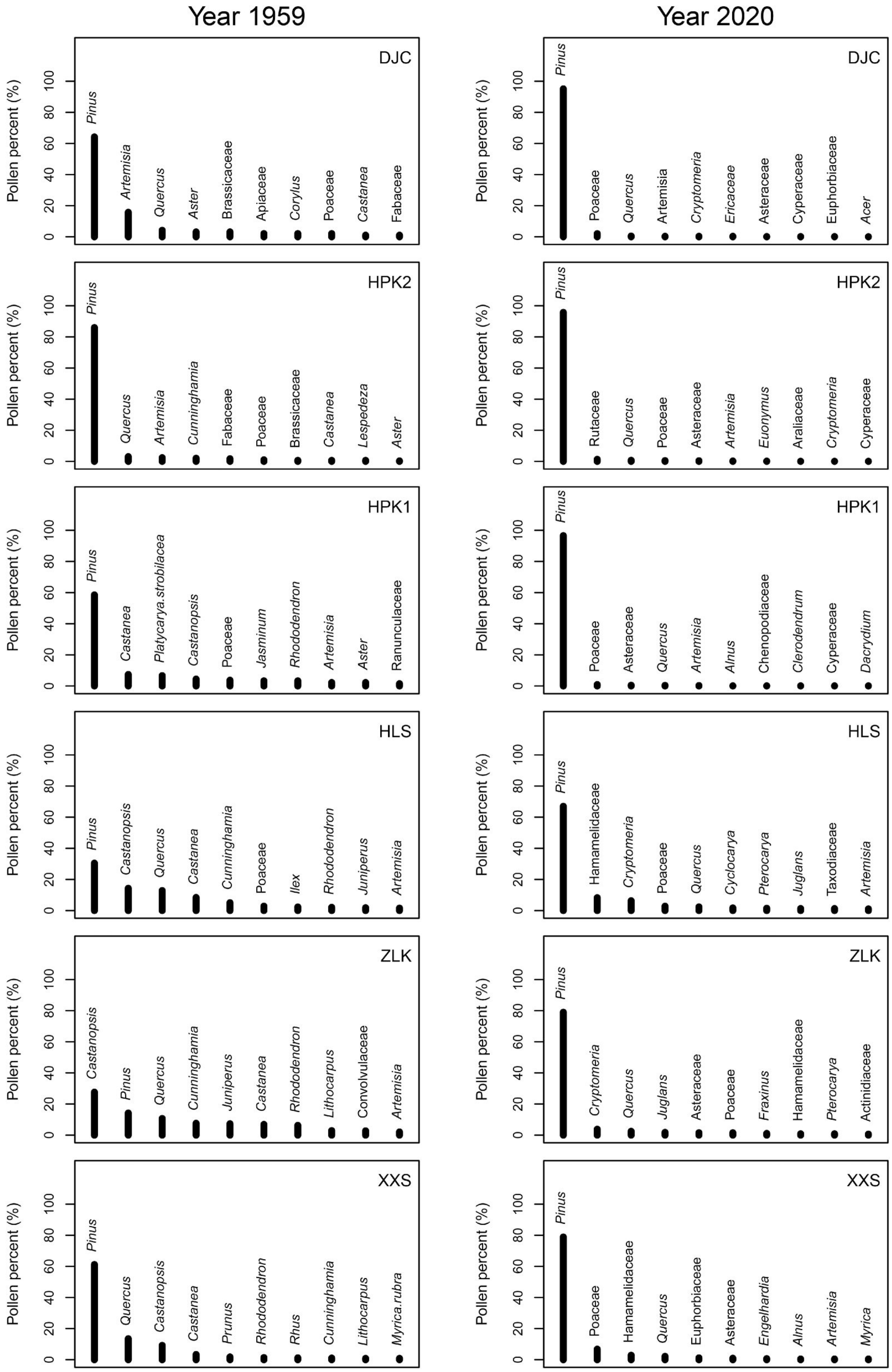

Figure 2. Differences of pollen assemblages for six sites between 1959 and 2020. Only ten most abundant pollen taxa are shown. Details of sampling sites are in Table 1.

(pollen percentage) at these sites on Lushan from 1959 to 2020 whereas two-thirds taxa decreased in abundances. Abundance changes for some representative taxa are shown in Table 3. Woody taxon, *Pinus*, has a significant increase in pollen abundance, whereas other woody taxa, *Castanea*, *Prunus*, and *Quercus*, decrease remarkably in abundance. For herbaceous taxa, the pollen abundance of *Artemisia* decreased significantly; however, the abundance of Poaceae pollen showed an increasing, but non-significant trend. Fabaceae pollen also has a significant decrease during 1959–2020.

Table 2. Reconstructed biomes in 1959 and 2020 of six sites on Lushan according to the PFT-Biome classifications of Zheng et al. (2023), Sun et al. (2020) and Ni et al. (2014).

		Zheng et al. 2023		Sun et al. 2020		Ni et al. 2014	
Sites	Threshold	2020	1959	2020	1959	2020	1959
XXS	0.1%	EBLF	DBLF	CLEC	WAMF	WTEM	WTEM
ZLK		EBLF	EBLF	WAMF	TSFO	WTEM	WTEM
HLS		DBLF	EBLF	WAMF	WAMF	WTEM	WTEM
HPK1		COMX	DBLF	CLEC	WAMF	WTEM	WTEM
HPK2		COMX	EBLF	CLEC	CLEC	WTEM	WTEM
DJC		COMX	DBLF	CLEC	CLEC	WTEM	WTEM
XXS	0.25%	EBLF	DBLF	CLEC	WAMF	WTEM	WTEM
ZLK		DBLF	EBLF	CLEC	TSFO	WTEM	WTEM
HLS		DBLF	EBLF	WAMF	WAMF	WTEM	WTEM
HPK1		COMX	EBLF	CLEC	WAMF	WTEM	WTEM
HPK2		COMX	EBLF	CLEC	CLEC	WTEM	WTEM
DJC		COMX	DBLF	CLEC	CLEC	WTEM	WTEM
XXS	0.5%	EBLF	DBLF	CLEC	WAMF	WTEM	WTEM
ZLK		DBLF	EBLF	CLEC	TSFO	WTEM	WTEM
HLS		DBLF	EBLF	CLEC	WAMF	WTEM	WTEM
HPK1		CLMX	EBLF	CLEC	CLEC	CLDE	WTEM
HPK2		COMX	EBLF	CLEC	CLEC	WTEM	WTEM
DJC		COMX	DBLF	CLEC	CLEC	WTEM	WTEM
XXS	0.75%	EBLF	DBLF	CLEC	CLEC	WTEM	WTEM
ZLK		DBLF	EBLF	CLEC	TSFO	WTEM	WTEM
HLS		DBLF	EBLF	CLEC	WAMF	WTEM	WTEM
HPK1		CLMX	EBLF	CLEC	CLEC	CLDE	WTEM
HPK2		COMX	EBLF	CLEC	CLEC	WTEM	WTEM
DJC		CLMX	DBLF	CLEC	CLEC	CLDE	WTEM
XXS	1%	DBLF	DBLF	CLEC	CLEC	WTEM	WTEM
ZLK		DBLF	EBLF	CLEC	TSFO	WTEM	WTEM
HLS		DBLF	EBLF	CLEC	WAMF	WTEM	WTEM
HPK1		CLMX	EBLF	CLEC	CLEC	CLDE	WTEM
HPK2		COMX	EBLF	CLEC	CLEC	WTEM	WTEM
DJC		CLMX	DBLF	CLEC	CLEC	CLDE	WTEM

The threshold of pollen percentage is set to 0.1%, 0.25%, 0.5%, 0.75% and 1%, separately. EBLF (Subtropical evergreen broadleaved forest), DBLF (Temperate deciduous broadleaved forest), COMX (Cool mixed forest) and CLMX (Cold mixed forest) are defined in Zheng et al. (2023). CLEC (Cold-temperate evergreen conifer forest), WAMF (North subtropical mixed forest) and TSFO (Tropical seasonal forest) are defined in Sun et al. (2020) WTEM (Warm–temperate evergreen broad-leaved and mixed forest) and CLDE (Cold deciduous forest) are defined in Ni et al. (2014).

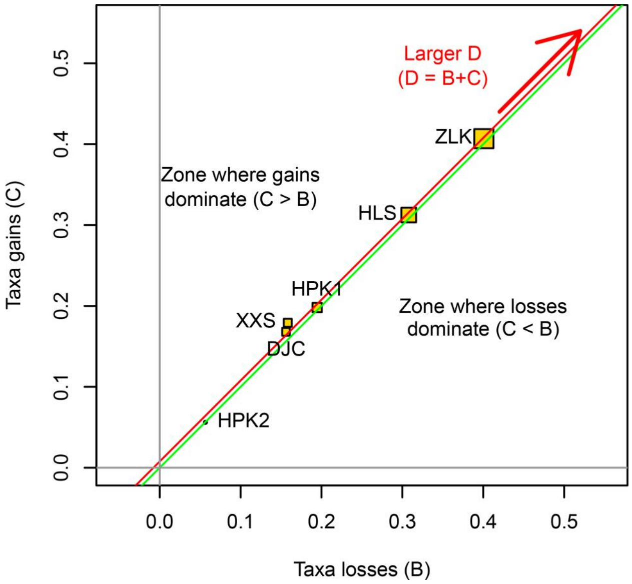

Figure 3. B-C plot for taxa abundance data, six sites on Lushan. Symbol diameters are proportional to the TBI statistics. The green line indicates that taxa gains (C) = taxa losses (B), slope = 1. The upper left of the green line indicates that the number of taxa gains is dominant (C > B), and the lower right indicates that the number of taxa losses is dominant (B > C). The red line was parallel to the green line, i.e. slope = 1. Its position above the green line indicates that, on average, taxa gains dominated losses between 1959 and 2020. Site names are the same as in Figure 1. Red arrow: direction where D = (B + C) increases.

Table 3. Changes in some representative taxa composition on Lushan from 1959 to 2020.

Taxon	Averaged abundance in 2020	Averaged abundance in 1959	Difference between 1959 and 2020	*p* Value
Pinus	85.40	52.45	32.95	**0.015**
Cryptomeria	1.69	0.00	1.69	0.257
Castanea	0.00	4.64	−4.64	**0.015**
Cyclocarya	0.29	0.00	0.29	0.501
Fraxinus	0.19	0.15	0.04	0.494
Hamamelidaceae	2.02	0.00	2.02	0.126
Prunus	0.00	1.01	−1.01	**0.031**
Quercus	1.38	7.53	−6.14	**0.016**
Ranunculaceae	0.00	0.41	−0.41	0.247
Rhododendron	0.00	2.20	−2.20	0.063
Rhus	0.00	0.56	−0.56	0.131
Rutaceae	0.22	0.00	0.22	0.499
Tilia	0.11	0.00	0.11	0.501
Artemisia	0.29	4.13	−3.84	**0.017**
Fabaceae	0.00	1.16	−1.16	**0.032**
Poaceae	2.45	1.61	0.84	0.377

The significance of bold values is 0.05.

4. Discussion

4.1. Vegetation changes or succession based on the palynological evidence

Comparing the main taxa of pollen assemblages in surface samples of 1959 and 2020, we found that pollen composition within the top ten pollen taxa exhibited remarkable discrepancies across the different elevation sites of Lushan. These discrepancies are not only reflected in low altitude vegetation belt (XXS), but also in high altitude vegetation belt (DJC). The increased abundance of *Pinus* pollen at all altitudes over the past 60 years might indicate the increase of plant cover of *Pinus* species in the vegetation communities on one hand; or respond to the increased pollen productivity of *Pinus* plants that grown from small to big trees on the other hand. In contrast, the abundance of *Quercus* pollen decreased for most of the sites during 1959–2020, except the site of HPK1. As the increasing number of *Pinus* plants or enlarged canopy for individuals, the space in a community may make room for *Pinus* species at the cost of *Quercus* and other species, i.e. the species rank could have been shifted (Collins et al. 2008). However, due to various pollen production and dispersal (Xu et al. 2007; Felde et al. 2014), caution must be taken when using pollen abundance indicating plant cover. Another decreased pollen taxon in abundance is *Castanea*. Again, *Pinus* plants phase-in and *Castanea* plants phase-out during community succession could also lead to the decrease of *Castanea* pollen. Further, human activity, like nuts collecting year on year deteriorates the natural growth of *Castanea* plants on Lushan (Li and Huang 1964).

4.2. Vegetation changes reflected by biomes

The reconstructed biomes for the sampling sites demonstrate that these reconstructions are not only affected by the way of pollen-PFTs-biome assignment, but also are sensitive to the pollen threshold value we chose. Ni et al. (2014) reconstructed the patterns of biome distribution over the last 22,000 yr in China. Within their pollen-PFTs-biome assignment, they defined 51 indicative PFTs belonging to 19 biomes for the whole range of China based on 2434 surface sites. Although some pollen taxa-PFTs relationships were modified, the version is much closer to the global PFT schemes (Prentice et al. 1996). Our biome reconstructions following the way of Ni et al. (2014) clearly showed the disadvantages of biomisation method applying to a local community simulation (Xu et al. 2015), because only WTEM (Warm–temperate evergreen broad-leaved and mixed forest) can be identified for pollen data of 1959 and for most cases of 2020. This means low resolution of biome reconstruction for the relatively short altitudinal gradient. Sun et al. (2020) updated the scheme of pollen-PFTs-biome assignment based on 1630 surface pollen sites in China and summarized the vegetation of China as 18 biomes containing 30 PFTs. In subtropics of China, the vegetation is composed of three biome types (southern subtropical broadleaved evergreen: STFO; middle subtropical broadleaf evergreen forest: MTFO; northern subtropical mixed forest: WAMF). Such classification is assumed to be more suitable to biome reconstruction for this special climatic zone (Sun et al. 2020). For current study, the biome reconstructions following Sun's way seem to show that the vegetation type at high altitude (HPK2 and DJC) did not change, keeping cold-temperate evergreen conifer forest through 60 years development. Whereas, vegetation at lower altitude (for XXS and ZLK with elevations below 600 m when pollen thresholds between 0.1% and 0.5%) might have changed during 1959–2020. At the same time, we must notice that the inappropriate assignment of pollen taxa to PFT could result in unreasonable biome reconstruction. This is also the original purpose of why Sun et al. (2020) updated the biomisation scheme, i.e. to obtain more reasonable vegetation reconstruction of China. Zheng et al. (2023) focused on the subtropical region across eastern China and established their own scheme of pollen taxa-PFTs-biome assignment, which includes 17 PFTs pertaining to 9 biomes. We reconstructed the basically convergent vegetation results for 1959: either EBLF (Subtropical evergreen broadleaved forest) or DBLF (Temperate deciduous broadleaved forest) that is obviously not in agreement with the descriptive vegetation of 1959 in Table 1. This controversy might further illustrate the limitation of the biomisation method that there is no direct relationship between pollen abundance and plant abundance (Cruz-Silva et al. 2022), unless quantitative vegetation surveys had been undertaken. However, the reconstructed vegetation in 2020 is more reasonable and somewhat in agreement with our observations (Observed vegetation in 2020, please see Table 1). From EBLF at low elevation, DBLF at middle elevation to COMX (Cool mixed forest) at high elevation, the vertical pattern of vegetation distribution on Lushan better displays the 'real' consequence of different forests succession over the past six decades. By using various levels of pollen threshold (from lowest 0.1% to highest 1%) and three ways of biomisation scheme, our exploration of vegetation reconstruction makes us have more confidence to draw a preliminary conclusion that the vertical vegetation spectrum has changed since 1959 on Lushan.

All in all, we are more inclined to the biome reconstruction results *via* the scheme of pollen taxa-PFTs-biome assignment put forwarded by Zheng et al. (2023) and by using the pollen threshold of 0.25%. This may be in related to several reasons. First, the study of Zheng et al. (2023) itself is focusing on the eastern China area and the design of PFT-biome classification is relatively more reasonable when discovering the evergreen/deciduous forest replacement. Second, the obscure situation of the altitudinal zonation for vegetation of 1950s could be seriously influenced by the characteristic of pollen data, which is mainly induced by long historical human disturbance. The phenomenon of ambiguous boundaries or the obscure vegetation zonation for secondary forests in vertical direction had been noticed earlier before, and this is especially true for eastern China (Da et al. 2009). Third, the vertical distributional patterns reflected by the reconstructed biomes on the basis of 2020 pollen data comprehensively correspond with the current thermal conditions on Lushan. In terms of biome, the striking changes of vegetation occurred most likely at the lowest altitude from highly human disturbed *Pinus massoniana* forest to evergreen broadleaved forest, and at the highest altitude from shrubland and meadow to cool mixed forest.

4.3. Temporal beta diversity

From the perspective of community composition, both XXS (the lowest site) and DJC (the highest site) have low taxa gains that could be attributed to the relatively high-level human disturbances. At low altitudinal area, local people relied on the tree branches as fuel for warming in winter, daily cooking and routine brick making etc. in 1950s. Similarly, people on Lushan settling down at high altitude consumed the forests as well for winter warming, cooking and house building etc. This human disturbance could be significant because Guling Town (nearby DJC) had been there decades ago and had a population from hundreds to thousands. Until 1981, the human-induced deforestation situation might slow down because the Lushan National Nature Reserve of Jiangxi was founded in that year (Liu and Wang 2010). The government prohibits tree cutting by propagating the legislative policy. While for ZLK, at 600 m, human activity might be light so the natural vegetation has the time to do normal restoration and succession. This reasonably explains why this site has significant taxa gain and the highest temporal beta diversity index (TBI). At HLS, forest dynamic has been also in a healthier condition and with the second largest TBI, probably in relation to a Buddha temple. People usually do protect the nearby forests around temple. HPK2 is the only site where taxa losses dominate during 1959–2020 with the lowest TBI.

The increased abundance for *Pinus* pollen at low altitude (e.g. XXS) is possibly and mainly from the contribution of *Pinus massoniana*. The forests of *Pinus massoniana* in olden days overlapping human planted *Pinus massoniana* (Zheng 1956; Li and Huang 1964) become patchy and mature conifer forests nowadays. However, the increased abundance for *Pinus* pollen at high altitude (over 900 m) is mostly from the

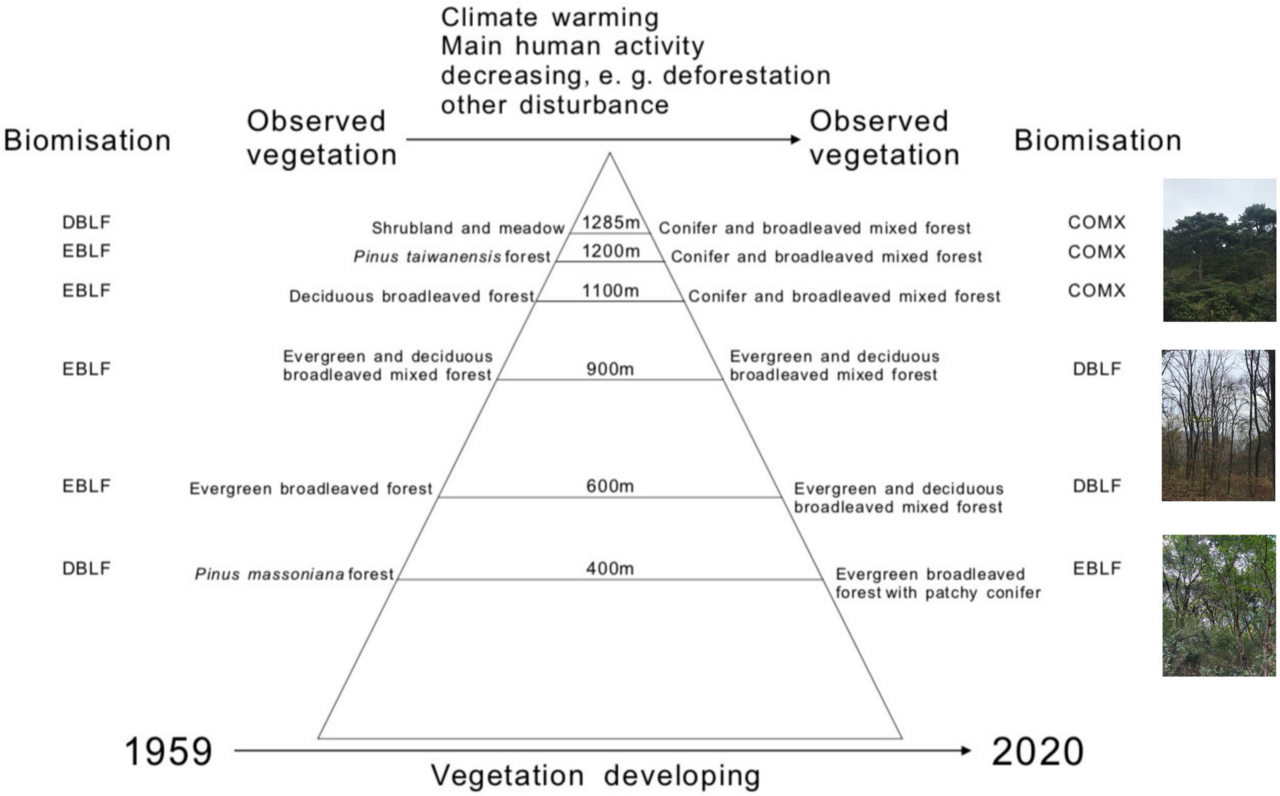

Figure 4. Schematic illustrations of vegetation changes on Lushan during 1959–2020. As climate warming, main human activity decreasing (e.g. deforestation) and other disturbance occur, vegetation of Lushan is developing over time. EBLF (Subtropical evergreen broadleaved forest), DBLF (Temperate deciduous broadleaved forest), COMX (Cool mixed forest) are defined in Zheng et al. (2023).

contribution of *Pinus taiwanensis* (Li and Huang 1964; Zhou et al. 2020). The distribution of these two species in different elevations is determined by their distinct thermal requirements in climate (Wang and Zhuo 1989; Fang et al. 2011). The increase of *Pinus* pollen for intermediate altitude site could be from multiple sources, given that the characteristic of *Pinus* pollen is anemophilous. The pollen spectrum of 2020 contains a certain amount of *Cryptomeria* pollen. For samples at mid altitude (especially the vicinity of HLS), *Cryptomeria* pollen is seriously in relation to the plantations of *C. japonica* established around 60 years ago (Zheng 1956; Du et al. 2014). In contrast, *Cryptomeria* pollen at high altitude might be briefly from the native and endemic species, *C. japonica var. sinensis* that lives in areas with higher elevation on Lushan. These gymnosperm species are quite important pioneer species in subtropical forest of China where they have shaped phylogenetic and functional tree community structure after heavy human disturbance, such as clear-cutting (Feng et al. 2014). Along with the succession of secondary forests over decades, conifer plants have prospered and could cause the decline of some broadleaved trees. The change of community composition and spatial structure can also influence the openness of forest, which is indicated by the fact that the vegetation was obviously much more open in 1959 (Li and Huang 1964) than the vegetation in 2020 for the whole Lushan. This situation may be reflected by the significant decreases of *Quercus* and *Artemisia* pollen.

4.4. Possible driving forces affecting vegetation dynamic

Over the past six decades, multiple potential forces have obviously driven vegetation dynamic on Lushan (Figure 4). Climate change has occurred because the mean annual temperature raised ca. 1.2 degree from 1960 to 2019 (Li et al. 2022). Such strong climatic force might be significant for some thermal-sensitive plant species, but almost no studies on specific plant migration along an altitudinal gradient on Lushan were conducted during this period. Thus, it is hard to know more on the change of community composition corresponding to the species migration. Human disturbance in Lushan forests is inevitable and always lasting since 1950s, although for the first 20 years (1959–1980) human-induced deforestation could be more serious than for the last 40 years (1981–2020) because of the effective implementation of protective forest policy (Liu et al. 2023b). More and more prospering tourism on Lushan in relation to the local infrastructure construction more or less made a negative effect on forests development. As for other forces, like landslides and pathogens also irregularly had taken place that they undoubtedly drove the vegetation structure (Dale et al. 2001), though their influence range sometimes is patchy and minor. Due to the steep slopes, landslides usually happened close to the road where the developing vegetation in its vicinity was destroyed somewhat. Pathogens indeed occurred on Lushan, mainly leading to the mortality of *Pinus* plants. When undergoing this biotic risk, local people usually cut down diseased *Pinus* species. This kind of forest management potentially altered the vegetation structure. However, the influence of selective logging is regarded as non-significant on species diversity in the succession process of forest, especially for secondary forests (Corlett 1994).

4.5. Implications for vegetation change on different timescales

Since subtropical primary forests in most low-elevation areas of east China have been destroyed due to historical human activities (Da et al. 2009; Qu et al. 2020), it is necessary to assess secondary succession of these damaged primary forests. Coupling the knowledge of vegetation change with the biodiversity redistribution is beneficial to develop reasonable strategies for sustainable ecosystem management (Cao et al. 2022; Pecl et al. 2017). Our study demonstrates that the vegetation on Lushan has remarkably changed over the past sixty decades; and multiple forces might drive secondary succession of these subtropical forests. Apart from climate warming, the human disturbance could be another main power. These findings are bridging ecologists and palaeoecologists to understand the vegetation (biome) change both for the short term (from day to year) and for the long term (from century to Quaternary). For example, evergreen forest replaced deciduous forest at higher mountains across eastern China (Zheng et al. 2023), which occurred during the period of Holocene warming and was discovered by the palynological evidence. This vegetation transformation was mainly driven by thermal condition. The current study as a case is kind of a manifestation of the abovementioned biome changes in the past. Lushan mountain is an individual and one of the most typical ecosystems in east China. The vegetation change over half a century obtained by pollen proxy is definitely a specific instance for improving the comprehension of the pollen-vegetation relationship for this region. However, how the pollen assembly we observed fits into the appropriate biomisation frameworks is a little bit tricky when using biomisation method, because we need to both carefully and reasonably interpret the past vegetation and spatial-temporal changes. Besides, due to ongoing climate warming accompanying with other driving factors, the dynamic of Lushan vegetation also has the vital implications for the projection of future forest shifts in subtropical Asia. As flash droughts have happened in east China (Zhang et al. 2017) and other regions worldwide (Yuan et al. 2023), and may be expanding to more land areas under higher-emission scenarios (i.e. SSP585, Yuan et al. 2023), the whole plant community composition on Lushan could be reordered. Consequently, the vegetation will transform again. This suggests that conservation biologists need to put more efforts to protect the representative vegetation belt, that is, evergreen broadleaved forest (Liu et al. 2023a).

5. Conclusions

The composition of pollen assemblages on Lushan from 1959 to 2020 has changed significantly across all altitudes, which lead to the reconstructed biomes quite divergent. Biomisation method and temporal beta diversity analysis can greatly assist to interpret the various phases of subtropical forest succession and the internal community dynamics. Although multiple forces could complicatedly drive the succession of the secondary forests, one sure thing is that the vegetation of Lushan nowadays has been very different from the past, i.e. 1950s.

Acknowledgments

We are thankful to Dr. Danqi Li, Lushan Botanical Garden, Jiangxi Province and Chinese Academy of Sciences for his help during the sampling campaign. We would also like to thank the anonymous reviewers for providing valuable feedback and suggestions; to Dr. Xin Xiong for reading the manuscript and offering helpful criticism.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This research was supported by Lushan Botanical Garden, Jiangxi Province and Chinese Academy of Sciences (grant numbers: 2019ZWZX03; 2021ZWZX26; 2022ZWZX04).

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