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Distribution and conservation of orchid species richness in China

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ABSTRACT

Orchidaceae, the orchid family, is one of the species richest families and the most endangered plant groups. Most orchids are narrowly distributed in specific habitats because of their mycorrhizal specificity, pollinator specialization and limited seed germination rate; compared to plants from other families, orchids are extremely susceptible to habitat disturbance. However, little is known about how orchids are distributed and how they are protected at large scales. In this study, we developed a distribution database for all the 1449 orchid species in China. Using this database, we explored patterns of orchid richness in relation to climate, net primary productivity and habitat heterogeneity in China. We then evaluated the *in situ* conservation status of the orchids in China by overlapping the species distribution and the terrestrial national and provincial nature reserves (NNRs and PNRs) in C\hina. We found that 90% of orchid species in China were distributed in 258,800 km^2 (2.7% of China's landmass). Net primary productivity, elevation range, and temperature seasonality together explained 34.4% of variance in orchid richness. On average, NNRs covered 12.1%, NNRs and PNRs together covered 29.1%, of orchid distribution areas. However, there were still 154 (including 83 endemic to China) narrowly distributed orchid species not covered by NNRs; and 48 (including 28 endemic to China) were not covered by either NNRs or PNRs. We proposed that nature reserves specifically designed for orchids need to be established in Southwest China and Hainan Island.

1. Introduction

Orchidaceae, the orchid family, is one of the species richest families of seed plants. It is composed of five subfamilies, 880 genera and more than 25,000 species in the world (Cribb et al., 2003). Many orchid species are important in horticultural for their charismatic flowers, and some species, such as *Gastrodia elata* and *Dendrobium offcinale*, have pretty high medical values especially in traditional Chinese medical science (Luo et al., 2003). Because orchids have mycorrhizal specificity, pollinator specialization and limited germination rates (Gravendeel et al., 2004; Cozzolino and Widmer, 2005; McCormick and Jacquemyn, 2014), most orchids are narrowly distributed in specific habitats (Lozano et al., 1996) and are extremely susceptible to habitat disturbance comparing to other plants (Cozzolino and Widmer, 2005; Jacquemyn et al., 2005, 2007). Currently, the orchid populations have been decreasing due to habitat loss and over-collection for ornament and medicine usage (Huang, 2011). In addition, Orchidaceae has a higher proportion of threatened genera and species than most other families (Pillon and Chase, 2007). The susceptibility and limited distribution may cause large-scale extinction events in orchids under future climate change (Swarts and Dixon, 2009). Considering its great value, endangered situation and its key role in ecosystem, Orchidaceae is frequently used as flagship group in biological conservation (Baillie et al., 2004). These characteristics make it important to explore the distribution and conservation status of orchids.

Orchids are widely distributed in the tropics and subtropics with different life forms (Cribb et al., 2003). Recent studies suggested that distribution of orchids were limited by the joint effect of habitat availability and pollination limitation (McCormick and Jacquemyn, 2014). Specifically, patterns of orchid richness are regulated by habitat size and elevation range at large scales (Jacquemyn et al., 2005; Schödelbauerová et al., 2009; Acharya et al., 2011), while by light availability, soil moisture, canopy height and area (especially for the epiphytic orchids) at fine scales (Gravendeel et al., 2004; Huang et al., 2008; McCormick and Jacquemyn, 2014). However, compared to the large number of orchid species, knowledge on the large-scale patterns and controls of orchid richness is limited (Chapman and Wang, 2002; Chen et al., 2009).

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Harboring more than 1300 orchids, China is one of the orchid richest countries in the world (Chen et al., 2009). The number is increasing as new species and varieties continued to be found (Liu et al., 2007). In China, orchids are distributed mainly in the southern to southwestern part of China, such as Yunnan, Sichuan and Taiwan Provinces (Chen et al., 2009). Most studies on orchids in China are focused on taxonomy and biogeography (Luo et al., 2003).

Facing the reality that a large number of species are at risk and the time and resources are limited, the primary way China employed for species conservation must be *in situ* conservation, thus setting up nature reserves (Heywood and Dulloo, 2005). Through *in situ* conservation, target species could be preserved along with its original habitat and genetic diversity (Ellstrand and Elam, 1993; Heywood and Dulloo, 2005). Up to 2012, China has set up more than 2600 nature reserves in order to protect its mega-biodiversity, including 363 national (NNRs) and 872 provincial nature reserves (PNRs) (Zhao et al., 2013). Unfortunately, there is no protection regulation for *in situ* conserving orchids (McBeath and McBeath, 2006). Among all these NNRs, only one, the "Yachang Orchid Nature Reserve", together with some PNRs, is specially designed for protecting orchids, albeit that most of the NNRs and PNRs have included different orchids (He et al., 2007). Besides, a recent evaluation based on species checklists of nature reserves illustrated that most of the orchids were not covered by nature reserves (Qin et al., 2012), thus, the protection of orchids in China is still a challenge. Therefore, it is of particular significance to strengthen the protection of the orchids in China.

In this study, we analyzed the distribution patterns of orchid richness and evaluated the *in situ* conservation status of orchids in China. To do this, we first compiled a distribution database of orchids and a spatial database of NNRs and PNRs in China. Based on these databases, together with other spatial databases of environments, we explored the patterns of orchid richness in relation to environments and identified the hotspots of orchid richness in China. We then evaluated the *in situ* protection status of orchids in China. The questions we asked were: (1) How orchid species were distributed and where were the hotspots located in China? (2) What environmental factors affected the distribution of orchid richness in China? (3) How orchids were protected in China?

2. Material and methods

2.1. Data collection

2.1.1. Distribution of orchids in China

We first compiled the county level occurrence for orchid species in China using all available literatures, such as national, provincial, local floras, checklists of nature reserves, monographs of field investigations for plants, and scientific articles, as well as specimen distribution records (www.cvh.ac.cn). The nomenclature of orchid checklist followed the recently published Flora of China (volume 25, Chen et al., 2009. Available at http://foc.eflora.cn/). Non-native species were excluded.

Since the county level occurrence may over-estimate the distribution of each species, we also collected the upper and lower elevation records and habitat type of each species to refine the distribution. We overlapped the county level occurrence with a vegetation map of China (1: 1,000,000) (Editorial Committee of Vegetation Map of China, 2007) and a digital elevation model (DEM) obtained from the United States Geological Survey (at a resolution of 30 m, available at http://reverb.echo.nasa.gov/reverb/redirect/wist). The distribution area is defined as the grid containing the habitat type and elevation between the upper and lower elevation of a species in the county where the species occurring. The orchid distributions were then transferred into grids at a resolution of 10×10 km. In total, the database contained 484,791 records of distribution girds for 1449 species (and varieties). We assigned life-form information for each species as terrestrial (748 species), epiphytic (688 species) and lithophytic (267 species) (some species have more than one life forms). We also assigned all the species as endemic (526 species) and non-endemic (923 species) to China according to their distributions.

We grouped the orchids into four types according to their range size, namely, most narrowly distributed quarter (Q1), narrowly distributed quarter (Q2), widely distributed quarter (Q3) and most widely distributed quarter (Q4).

2.1.2. Environmental factors

We used climate, productivity and habitat heterogeneity as possible determinants of large-scale patterns of orchid richness in China. Climatic data were obtained from the WorldClim database (Hijmans et al., 2005. Available at: http://www.worldclim.org/). We used the following climatic variables to explore the influence of climate on the orchid richness in China: mean annual temperature (MAT, °C), mean temperature of the warmest (MTWM, °C) and coldest month (MTCM, °C), potential evapotranspiration (PET, mm), actual evapotranspiration (AET, mm), mean annual precipitation (MAP, mm), growing season precipitation (GSP, mm; defined as precipitation between May and October), moisture index (IM, unitless), seasonality of temperature (TSN, unitless) and precipitation (PSN, unitless), and annual range of temperature(ART, °C).

We used the satellite based net primary productivity (MODIS-NPP, g C m^2, available at: ftp://e4ftl01.cr.usgs.gov) to represent productivity.

We used elevation range (RELE, m, defined as the difference between the highest and lowest elevation in the grid, calculated based on the USGS-DEM) and number of vegetation types (VGT, defined as number of natural associations based on the vegetation map of China of 1: 1,000,000) in each 10×10 km grid as surrogates of habitat heterogeneity.

We calculated all the aforementioned environments by overlapping the 10×10 km grid system with spatial distribution of these variables using a geographical information system (ArcGIS 10.0, ESRI, 2012).

2.1.3. Spatial database of nature reserves in China

Among the 2600 nature reserves in China, 319 NNRs covering 9.4×10^5 km^2 (~10% of the total landmass), and 835 PNRs covering 3.7×10^5 km^2 (~4% of the total landmass), are terrestrial ones. To evaluate the representativeness of orchids in the nature reserves, we compiled the spatial database on NNRs and PNRs (Zhao et al., 2013) by digitalizing all terrestrial NNRs and PNRs through the geographical information system software ArcGIS 10.0 (ESRI, 2012).

2.2. Data analysis

2.2.1. Hotspots identification

Species richness for each gird was calculated as the total number of species in the grid. Complementary algorithm (Dobson, 1997) was applied to identify hotspots of orchid richness in China. The basic idea of this algorithm is recognizing the minimum number of grids that could cover all the species. Grid with the highest species richness was selected first, and then grid with the highest number of the remaining (unselected) species was selected. The process continued iteratively until all species were included in the selected grids (Dobson, 1997). Grids including 90% species (i.e. 1304 out of 1449 species in this study) were set as hotspots (Kati et al., 2004).

2.2.2. Species richness-environmental relationship

We first applied simple linear regression to explore the relationship between single environmental factor and species richness. We then applied a stepwise regression to explore the combined effects of environmental factors on orchid richness by the following steps. First, the best single predictor for the species richness was kept in the model; then all significant single factors were added to the model, and the Akaike information criterion (AIC) was applied to evaluate the goodness of the fit of the models. We also applied variation partition approach to compare the effects of climate vs. NPP. To do this, we built three models, first a full model containing all NPP and climatic variables; second, a pure climate model only containing the climatic variables; third, a pure NPP model only containing NPP. The variance of orchid richness was divided into four different components according to the results of the three models: independent effect of climate, independent effect of NPP, joint effect of climate and NPP, and unexplained component (Wang et al., 2011). We used adjusted R^2 to estimate explanatory power of each component as we had different numbers of explanatory variables in our models. The variation partition is also applied to compare the effects of climate plus NPP vs. habitat heterogeneity. We explored the relationship between environmental factors and species richness of overall species and of different life forms, and also for richness of endemic and non-endemic species.

2.2.3. Representativeness of orchids in nature reserves

We evaluated the representativeness of each orchid by calculating the proportion of distribution area covered by the NNRs and by both NNRs and PNRs. To do this, we overlaid the distribution map with the NNRs and PNRs maps for each species. The protection rate of each species is defined as ratio of the area covered by NNRs and PNRs to the total distributed area of the species. We calculated the protection rate of each species covered by NNRs and by NNRs and PNRs together.

All statistical analyses were carried out using R 2.15.1 (http://www.r-project.org/).

3. Result

3.1. Geographical patterns of orchid richness in China

As a whole, orchid richness was highest in the Southwest China, with >100 species in each grid, and lowest in the Tibetan Plateau, Xinjiang Region and the western Inner Mongolia, without any orchids in most grids. The orchid richness was also low in the plain areas, such as the North China Plain, the Northeast China Plain and the Middle and Lower Yangtze Plain (Fig. 1a). For different life forms, the terrestrial orchids showed the same pattern as the overall orchids (Fig. 1b), whereas the epiphytic and lithophytic orchids were mostly distributed in the Southwest China (Fig. 1c and d). The non-endemic orchids showed the same pattern as overall orchids (Fig. 1e), while the endemic ones were mostly distributed in the Southwest China (Fig. 1f).

The complementary algorithm depicted that 6762 grids (a total area of $\sim 6.8 \times 10^5$ km^2, or 7% of China's landmass) included all orchid species in China, with 2588 grids ($\sim 2.6 \times 10^5$ km^2, or 2.7% of the landmass) included 90% of the orchid species. Accordingly, the complementary algorithm identifies these 2588 grids as hotspots, which were mostly distributed in the following regions: western Yunnan, mid-western Guangxi, western Hainan, southeastern Sichuan and the mountainous area of Taiwan (Fig. 2).

3.2. Relationship between orchid species richness and environmental variables

Richness of overall orchids was significantly correlated with nearly all variables. The strongest single predictor, NPP, explained 24.5% ($p < 0.001$) of the variance in species richness. The strongest predictors among the environmental energy, water availability, climatic seasonality, and habitat heterogeneity were MTCM ($R^2 = 4.4\%$, $p < 0.001$), IM ($R^2 = 16.2\%$, $p < 0.001$), TSN ($R^2 = 13.2\%$, $p < 0.001$) and RELE ($R^2 = 13.7\%$, $p < 0.001$), respectively (Table 1).

Richness of different life forms exhibited nearly the same patterns along the environmental gradients, and the single best predictor for different life forms remained to be NPP. For terrestrial orchids, NPP explained 19.4% ($p < 0.001$) of the variance in species richness; the strongest predictors among the environmental energy, water availability, climatic seasonality, and habitat heterogeneity were MTWM ($R^2 = 3.2\%$, $p < 0.001$), IM ($R^2 = 14.9\%$, $p < 0.001$), TSN ($R^2 = 9.2\%$, $p < 0.001$) and RELE ($R^2 = 14.1\%$, $p < 0.001$), respectively (Table 1). For epiphytic orchids, NPP explained 27.5% ($p < 0.001$) of the variance in species richness; the strongest predictors among the environmental energy, water availability, climatic seasonality, and habitat heterogeneity were MTCM ($R^2 = 4.1\%$, $p < 0.001$), GSP ($R^2 = 10.5\%$, $p < 0.001$), TSN ($R^2 = 24.8\%$, $p < 0.001$) and RELE ($R^2 = 8.5\%$, $p < 0.001$), respectively (Table 1). For lithophytic orchids, NPP explained 21.5% ($p < 0.001$) of the variance in species richness; the strongest predictors among the environmental energy, water availability, climatic seasonality, and habitat heterogeneity were MTCM ($R^2 = 5.2\%$, $p < 0.001$), GSP ($R^2 = 9.9\%$, $p < 0.001$), TSN ($R^2 = 20.4\%$, $p < 0.001$) and RELE ($R^2 = 6.7\%$, $p < 0.001$), respectively (Table 1).

For richness of orchids endemic to China, the strongest single predictor, TSN, explained 25.7% ($p < 0.001$) of the variance in species richness; the strongest predictors among the environmental energy, water availability, productivity and habitat heterogeneity were MTCM ($R^2 = 9.2\%$, $p < 0.001$), IM ($R^2 = 18.6\%$, $p < 0.001$), NPP ($R^2 = 9.4\%$, $p < 0.001$) and RELE ($R^2 = 20.6\%$, $p < 0.001$), respectively (Table 1). The strongest single predictor for richness of non-endemic orchids was NPP ($R^2 = 25.1\%$, $p < 0.001$); with MTCM ($R^2 = 6.2\%$, $p < 0.001$), GSP ($R^2 = 15.2\%$, $p < 0.001$), TSN ($R^2 = 14.5\%$, $p < 0.001$) and RELE ($R^2 = 12.5\%$, $p < 0.001$) as the strongest predictors among the environmental energy, water availability, climatic seasonality, and habitat heterogeneity, respectively (Table 1).

Stepwise regression showed that NPP, RELE, and TSN together explained 34.4% of variance in the overall orchid richness. For richness of orchids with different life forms, RELE, NPP, IM explained 29.7% of the variance in terrestrial orchids; NPP, TSN and RELE explained 36.3% of the variance in epiphytic orchids; NPP, TSN and RELE explained 28.8% of the variance in lithophytic orchids. For richness of orchids with different types of endemism, NPP, TSN and RELE explained 36.4% of the variance in endemic orchids; and NPP, RELE and TSN explained 35.1% of the variance in non-endemic orchids (Table 2).

A variation partitioning illustrated that the independent effects of NPP and climate explained 24.5% and 27.0%, their joint effect explained 34.2% of the variance, respectively (Fig. 3a). The breakdowns were 19.4%, 22.9%, 28.2% for terrestrial orchids, 27.5%, 32.0%, 41.0% for epiphytic orchids, and 21.5%, 25.2%, 32.8% for lithophytic orchids, respectively (Fig. 3b–d). When the habitat heterogeneity was considered, the independent effects of NPP plus climate and habitat heterogeneity explained 34.2% and 14.0%, their joint effect explained 36.8% of the variance, respectively (Fig. 3e). The breakdowns were 28.2%, 14.7%, 31.7% for terrestrial orchids, 41.0%, 8.7%, 41.8% for epiphytic orchids, and 32.8%, 6.9%, 34.2% for lithophytic orchids, respectively (Fig. 3f–h).

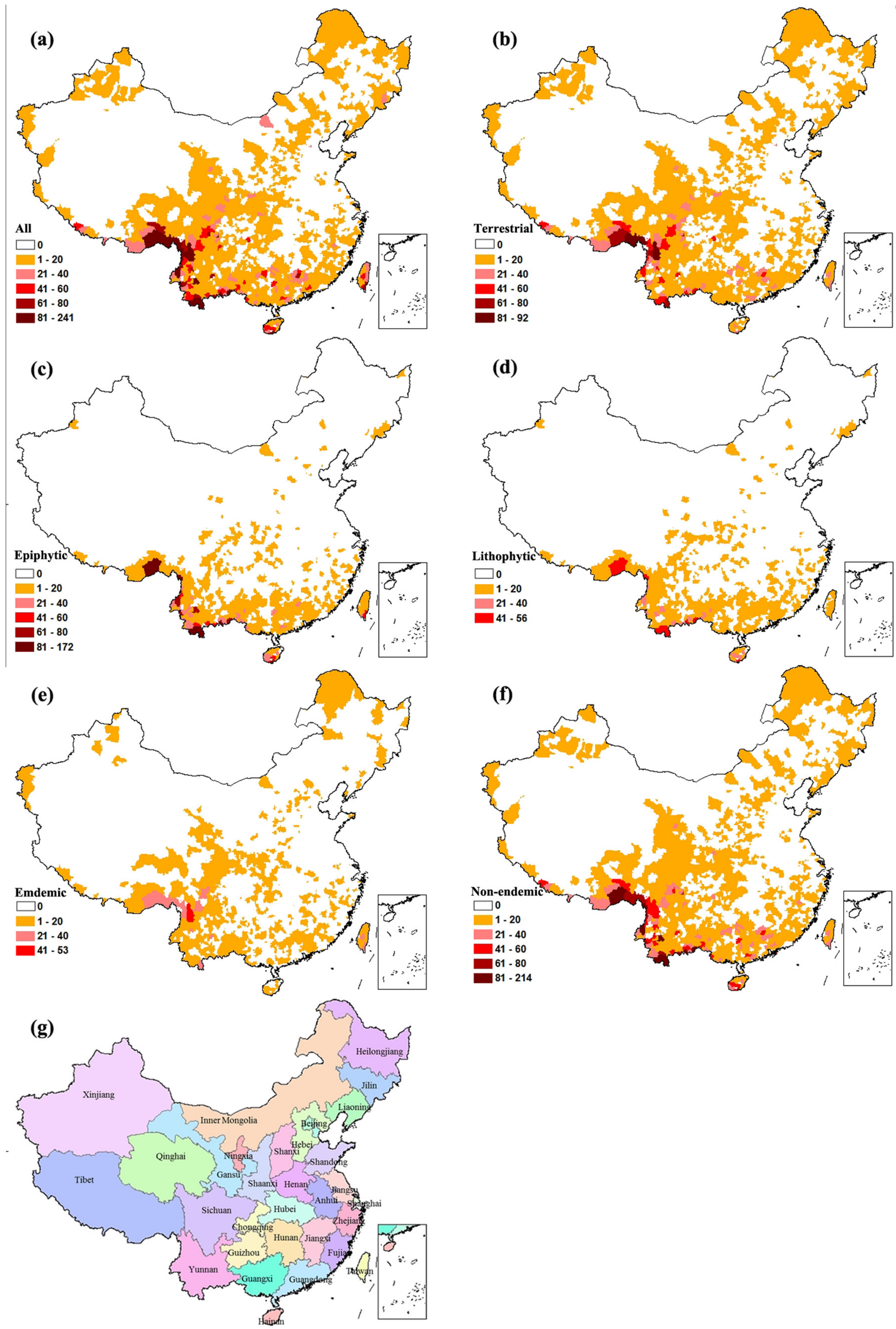

Fig. 1. Distribution of orchid richness in China: (a) all orchids, (b) terrestrial orchids, (c) epiphytic orchids, (d) lithophytic orchids, (e) orchids endemic to China, and (f) orchids non-endemic to China. The sub-figure (g) illustrated the provinces of China.

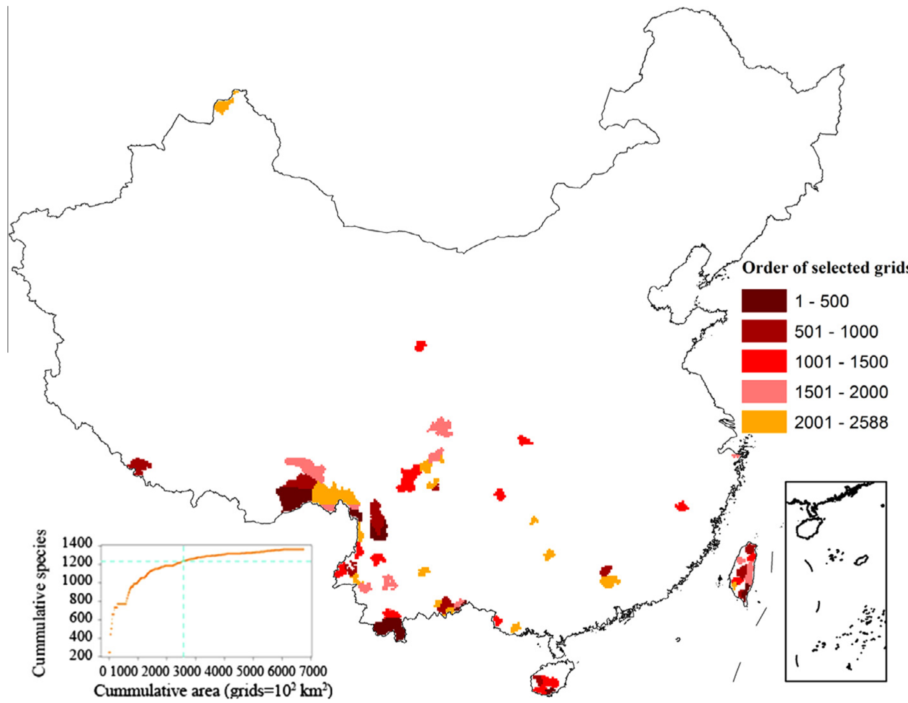

Fig. 2. Hotspots of orchid richness in China based on the complementary algorithm. The number for each grid indicated the order of selection by the complementary algorithm. The subset figure showed the increment of cumulative species richness with the number of selected grids by the complementary algorithm.

Table 1
Correlation between orchid richness and environmental variables in China (R^2, %).

	Overall	Terrestrial	Epiphytic	Lithophytic	Endemic	Non-endemic
No. of species	1449	748	688	267	526	923
Environmental energy						
MAT (°C)	1.9**	0.3 ***	1.5***	2.5***	3.5***	3.3***
MTWM (°C)	1.8***	3.2***	2.2***	0.6 ***	3.5***	0.9**
MTCM (°C)	4.4***	1.8***	4.1***	5.2***	9.2***	6.1***
PET (mm)	0.5***	0.0 ^{NS}	0.3***	20.9 ***	0.3***	1.4***
Water availability						
AET (mm)	4.5***	2.1***	0.7***	1.5***	1.7***	5.7***
MAP (mm)	9.2***	5.9***	4.6***	4.4***	8***	9.9***
IM (unitless)	16.2***	14.9***	5.8***	3.7***	18.6***	14.4***
GSP (mm)	14.0***	9.4***	10.5***	9.9***	12.5***	15.2***
Climatic seasonality						
ART (°C)	10.8***	7.1***	17.0***	15.8***	20.1***	12.4***
TSN (unitless)	13.2***	9.3***	24.8***	20.4***	25.7***	14.7***
PSN (unitless)	0.2***	0.3***	1.8***	1.4***	0.0 ^{NS}	0.1***
Productivity						
NPP (g C m^2)	24.5***	19.4***	27.5***	21.5***	9.4***	25.1***
Habitat heterogeneity						
RELE (m)	13.7***	14.1***	8.5***	6.6***	20.6***	12.5***
VGT(unitless)	0.8***	1.2***	0.2***	0.1***	0.4***	0.6***

^{NS} $p > 0.05$; $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.
Abbreviations: MAT = mean annual temperature, MTWM = mean temperature of the warmest month, MTCM = mean temperature of the coldest month, PET = potential evapotranspiration, GSP = growing-season precipitation (from May to October), AET = actual evapotranspiration, MAP = mean annual precipitation, IM = moisture index, ART = annual range of temperature, TSN = temperature seasonality, PSN = precipitation seasonality, NPP = net primary production, RELE = elevational range, VGT = number of vegetation types.

3.3. Representativeness of orchids in the NNRs and PNRs in China

On average, NNRs covered 12.1% (std = 16%) of distribution areas for all orchids in China. The protection coverage was higher in the most narrowly (Q1, mean = 14.6%) and narrowly distributed orchids (Q2, 14.8%) than the widely (Q3, 10.4%) and the most widely distributed orchids (Q4, 8.9%). One hundred and fifty four species were not covered by any NNR in China, including one most widely distributed (Q4), 10 widely distributed (Q3), 34 narrowly distributed (Q2), and 109 most narrowly distributed (Q1) orchids (Fig. 4a). Among these unprotected orchids, 83 were endemic to China.

NNRs and PNRs together covered 29.1% (std = 16%) of distribution areas for all orchids in China. The protection coverage was higher in the most narrowly (Q1, mean = 29.4%) and narrowly distributed orchids (Q2, 32.8%) than the widely (Q3, 27.2%) and the

Table 2
Stepwise regression models showing determinant factors for richness of different orchid groups in China.

Orchid groups	Predictors	Cum. R^2	AIC
Overall	NPP	24.5%	8833.2
	RELE	33%	4294.2
	TSN	34.4%	3503.0
Terrestrial	NPP	19.4%	3603.1
	RELE	29.0%	−980.1
	IM	29.7%	−1433.2
Epiphytic	NPP	27.5%	3303.2
	TSN	34.9%	1921.2
	RELE	36.3%	1635.7
Lithophytic	NPP	21.4%	42.5
	TSN	27.9%	−1069.3
	RELE	28.8%	−1245.8
Endemic	RELE	20.6%	−4504.9
	TSN	32.5%	−8122.9
	IM	36.4%	−9432.0
Non-endemic	NPP	25.1%	4249.4
	RELE	33.0%	292.3
	TSN	35.1%	−905.7

Refer to Table 1 for the abbreviations.

most widely distributed orchids (Q4, 26.9%). There were still 48 species (28 were endemic to China) that were covered neither by NNR nor by PNR in China, including three narrowly distributed (Q2), and 45 most narrowly distributed (Q1) orchids (Fig. 4b).

These unprotected orchids by NNRs were mostly distributed in the Southwest China and Hainan Island, some grids in the Southeast China, central China and Northeast China also contained some unprotected orchids (Fig. 5a). When the PNRs were considered, unprotected orchids were mostly distributed in the Southwest China, mainly in Yunnan, Guizhou and Guangxi Provinces (Fig. 5b).

4. Discussion

4.1. Distribution patterns of orchid richness in China

Orchid family is one of the species richest families and one of the most endangered groups worldwide (Cribb et al., 2003). In this study, we explored the distribution patterns of orchid richness and evaluated the *in situ* conservation of orchids in China. We found that the highest orchid species occurred in the Southwestern China and Hainan Island, but the lowest in the Tibetan Plateau, Xinjiang Region and the western part of Inner Mongolia. The pattern of orchid richness is coincident with that of other groups in China (López-Pujol et al., 2006; Tang et al. 2006; Zhang and Ma, 2008; Wang et al., 2011). Furthermore, the hotspots of orchids are mainly located in the mountainous areas, which is consistent with Tang et al. (2006), possibly because mountains provide heterogeneous habitats for different species. These results indicated that the distribution of orchid richness followed a general pattern of other plant groups in China.

Consistent with many previous studies on the richness patterns of different groups (Waide et al., 1999; Pärtel et al., 2007), we

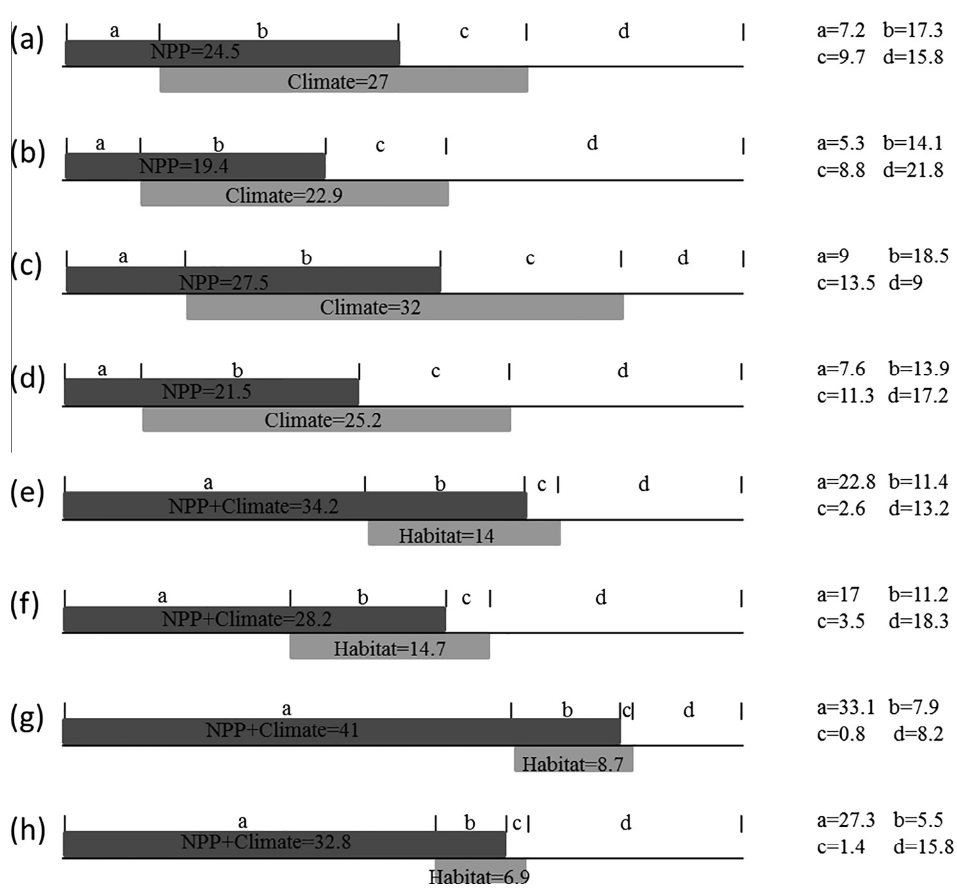

Fig. 3. The partitioning of the deviance in orchid species richness using partial regression for the comparing effects of climates vs. NPP (a–d): (a) all, (b) terrestrial, (c) epiphytic, (d) lithophytic; and the effects of climate plus NPP vs. habitat heterogeneity (e–h): (e) all, (f) terrestrial, (g) epiphytic, (h) lithophytic. In each sub-figure, a, and c are the independent, b is the co-varying, components of two groups of factors, d is residual deviance, respectively.

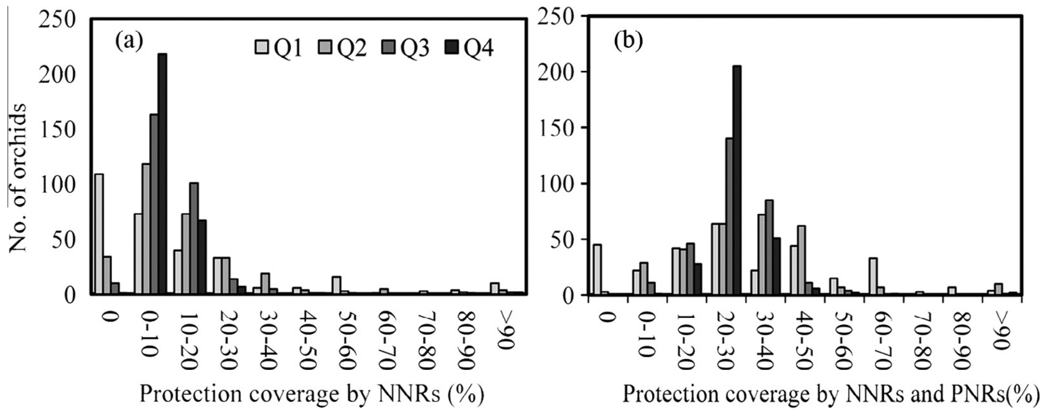

Fig. 4. Frequency distribution of percentage of orchids covered by national nature reserves (NNRs) (a) and by both national and provincial nature reserves (NNRs and PNRs) (b) in China for orchids with different range sizes. Q1: most narrowly distributed, Q2: narrowly distributed, Q3: widely distributed, and Q4: most widely distributed.

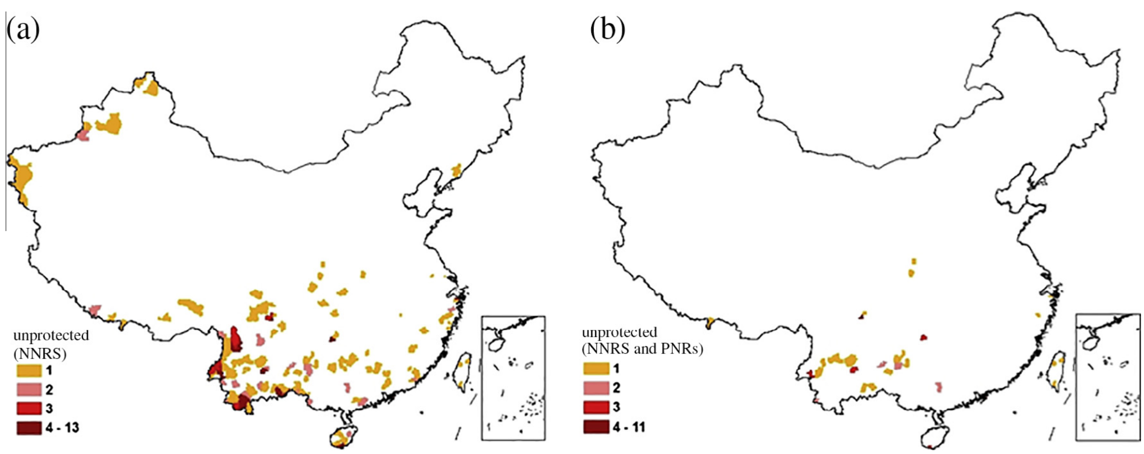

Fig. 5. Distribution of richness of orchids not covered by national nature reserves (a) and by either national or provincial nature reserves (b) in China.

found that NPP was the single best predictor of orchid richness in China. NPP may enhance orchid richness through the following two ways. First, high NPP means large population size for a given species, thus allows more individuals and more diverse genes to co-exist (Gaston, 2000; Clarke and Gaston 2006), these characteristics allows a species to survive in more heterogeneous environments (Wright, 1983); this strategy, in some extent, further creates larger gap of segregation among species, accelerating the speciation process of the region (Hubbell, 2001). Second, high NPP provides habitats and food for diverse insects (DeLucia et al, 2014), thus increases orchid richness, as most orchids are pollinated by specific insects (Kelly et al, 2013).

Climate is by far the most important factor regulating richness of orchids in China (Fig. 3; Table 2). Among the climatic factors, we found relative important roles of temperature seasonality (TSN) and coldness (MTCM) influencing the orchid richness in China (Tables 1 and 2). It is reported that most orchids survived in a particular range of temperature (Blanchard and Runkle, 2006). The optimal daily mean temperature for orchids is between 14 and 17 °C for all seasons, although some may tolerate temperature as low as 4 °C (Blanchard and Runkle, 2006; Lee et al., 2007; Acharya et al., 2011). Therefore a relatively stable temperature (low ART or TSN) is necessary for orchid. Under a stable climate, energy consumed for species' internal adjustment declines, leaving more energy for reproduction and thus enhances richness (Connell et al., 1964). We also found that winter coldness (represented by MTCM) accounted for much more variation in orchid richness than the other energy variables (Table 1). From a historical point of view, the winter coldness played more important roles for tropics originated species than the temperate originated species (Wang et al., 2011). Winter coldness may influence the distribution of orchids in the following ways. First, flower blossom and seed germination of orchids are very sensitive to the ambient temperature (Acharya et al., 2011). Second, most orchids are pollinated by specific insects, which is also very sensitive to the winter coldness (Nilsson, 1992; Phillips et al., 2011). Because of the sensitivity to winter coldness, climate warming is generally favorable for the population development of many orchid species (Blinova, 2008).

Besides climate, habitat heterogeneity also contributes significantly to the distributions of orchid species in China. Given that the habitat requirement may vary among orchid species (Michael and Chase, 2009), areas with great elevation range could provide a variety of habitat conditions, thus contain more species. Consistent with Huang et al. (2012), we found that the influence of elevation range is more significant on the richness of endemic orchid species than on that of non-endemic orchids. It is reasonable that heterogeneous habitat promotes the diversity of species endemic to a specific region, as it might result in dispersal barriers and accelerate speciation and differentiation (Lomolino et al., 2006).

Since most orchids have symbiotic relationship with mycorrhizal fungi and are pollinated by specific insects (Huang et al., 2008), the explanatory power of the environmental models is relative low (28.8–36.4%) compared to other plant groups (Wang et al., 2011). Factors controlling distribution of the mycorrhizal fungi and the pollinators also influence the distribution of orchid richness (Phillips et al., 2011). However, detailed research about these microenvironments, such as light availability, soil properties and pollinator presence, were beyond our analysis.

4.2. Conservation of orchids in China

Same as the situation in other areas across the world, over-collection, habitat fragmentation and destruction are major factors driving a great number of orchid species in China to extinction (Martha et al, 2010; Qin et al., 2012). Even if we set aside orchids' great ornamental and medical values, their dependence on specific fungi and pollinators could be devastating for them (Phillips et al, 2014). Under this circumstance, establishing related nature reserves and conserving the whole ecosystem *in situ* is the most effective way to promote conservation of orchids.

According to our study, ~90% of orchids are represented in national nature reserves (NNRs), and provincial nature reserves (PNRs) covered another ~7%. The protection status of orchids is better than a recently evaluation based on checklist of nature reserves (Qin et al., 2012), which reported that only 676 orchid species (accounts for 50.7% of the total species number in that study) have been covered by nature reserves in China. Qin's study underestimated the coverage of orchids in nature reserves, partly because of the following two reasons. First, the checklists are incomplete in some natural reserves (e.g. Zhang and Yang, 2001), which may underestimate the conservation status. Second, Qin's study based on only 543 nature reserves of China (accounts for 20.9% of all nature reserves in China) and adopted expert consulting method to evaluate the protection status; subjectivity and limitation of information brought by such method and data may weaken the study's reliability.

Even though, there are still 154 species (10.6% of our study species, including 83 endemic to China) that are totally unprotected by NNRs, as well as 48 species (3.3% of our study species, including 28 endemic to China) that are protected by neither NNRs nor PNRs. Most of these unprotected species distribute in a relatively small area (Fig. 4) in the Southwestern China and Hainan Island (Fig. 5a and b) and more than half are endemic to China. Although it is unrealistic to protect every orchid species in China due to the limitation of resources, it is necessary to study the current population status of the unprotected orchid species (see Appendix). Besides, our results highlight the importance of the Southwestern China and Hainan Island in the conservation of orchid species for the overlapping of hotspots and species rich area in these regions. We therefore propose that nature reserves specifically designed for orchids need to be set in these areas.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2014.10.026.

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