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The impact of secondary forest restoration on multiple ecosystem services and their trade-offs

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ABSTRACT

Secondary forests have received more attention in recent decades because their total area is increasing and the greater recognition of ecological and economical benefits provided by forest ecosystems. Therefore, the Chinese government has given high priority to implementing its Natural Forest Program that includes the restoration of degraded secondary forests. Hence, how ecosystem services (ESs) and their trade-offs are altered during the restoration process of secondary forests merits research. Here, we selected five key ecological indicators of forests, namely plant diversity and four ESs—air quality regulation, maintenance of soil fertility, global climate regulation, and timber provisioning—to examine the trends and patterns in the variation of multiple indicators and their trade-offs during forest restoration. Furthermore, secondary forests in subtropical China are characterized by a diverse tree species community that transitions from conifers in the early stage of restoration, to deciduous broadleaf and evergreen broadleaf species in its mid and late stages; this provides an excellent opportunity to investigate the influences of different tree functional groups on ESs and the trade-offs among them. Our results showed that late-forest had a greater capacity to supply higher and more evenly distributed benefits of ESs than did early or mid-stage restored forests. We also found that the magnitude of trade-offs between paired ESs changed with the stage of restoration. Furthermore, the variation of the beneficiary in critical trade-offs corresponded to the patterns of change in benefits of specific ESs. Trade-offs between plant diversity and other ESs were significantly influenced by tree functional group, in that the deciduous broadleaved species had significant positive effects whereas the conifer and evergreen broadleaved species had negative effects. We conclude that accurate prediction and management of ESs in restoration forests should explicitly account for tree functional groups, in addition to the effects from combined trade-offs among multiple ESs.

1. Introduction

Areas of secondary forests converted from primary ones have gradually increased owing to the high intensity of human disturbances in recent decades (Xiang et al., 2016). Nevertheless, secondary forests retain great potential for providing multiple goods and ecological services (ESs), so they garnered much attention as very important forest resources late in the 20th century (Chokkalingam and de Jong, 2001). Since then, the restoration and smart management of secondary forests has become one of the most popular research topics among science and policy communities, largely because ecological restoration programs have been shown to elicit positive outcomes for both biodiversity and the provisioning of multiple ESs in a range of investigated ecosystems (Chokkalingam and de Jong, 2001; Turner et al., 2007; Benayas et al., 2009; Carpenter et al., 2009; Barral et al., 2015). In China, secondary forests are widely dispersed and vary in type, occupying 46.7% of the national forestry area. The Chinese government has thus given high priority to resource conservation and environmental protection through the implementation of ecological restoration projects, such as the Grain-for-Green program, afforestation campaigns, and the restoration of degraded secondary forests (Rozelle et al., 2003; Grebner et al., 2013; Wang et al., 2017). Like many other ecological management

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programs, it is crucial to learn from ongoing projects which practices and factors lead to success or failure in forest restoration and their supply of ESs (Carpenter et al., 2009; Daily et al., 2009). In the subtropical region of southern China, most of the primary evergreen broadleaved forests are now replaced by secondary forests, with variation in disturbance intensity leaving restored secondary forests in a range of different stages of successional development (Chen and Kurokawa, 2005; Xiang et al., 2016; Zeng et al., 2017). Investigating the variation of multiple ESs along the restoration gradients of secondary forests could provide valuable and useful information to improve the design and implementation of forest restoration programs (Tallis et al., 2008; Wang et al., 2017).

Although scientists and policymakers presume that ESs increase in response to one type of management activity through a synergistic process, it is widely accepted that human activities designed to improve a specific ES will probably lead to one or more trade-offs with other ESs (Egoh et al., 2008; Bennett et al., 2009; Raudsepp-Hearne et al., 2010; Haase et al., 2012; Maskell et al., 2013). For example, local residents may seek to augment timber production via more frequent logging and the planting of faster-growing tree species, but important trade-offs could exist between the provisioning services (timber production) and biodiversity and air quality regulation if those replacement tree species have smaller leaf areas (Grebner et al., 2013; Onaindia et al., 2013). Therefore, one reason for the failed outcomes of restoration programs aiming to improve ESs is that trade-off relationships may ensue among multiple ESs (Carpenter et al., 2009). In subtropical China, the management objectives of secondary forests in general are twofold: biodiversity conservation and an overall improvement in ES benefits. The quantification of single and overall benefits and trade-offs among multiple, potentially conflicting ESs is essential for gauging progress in meeting ES objectives. In this respect, trade-off analysis allows a detailed understanding of ecosystem dynamics and associated mechanisms necessary for the establishment of adaptive ES management programs (Bradford and D'Amato, 2012; Goldstein et al., 2012; Galicia and Zarco-Arista, 2014). However, few studies have developed robust approaches for quantifying and evaluating possible trade-offs among multiple ESs along a restoration gradient, either at the stand level or whole forest (Dickie et al., 2011; Maskell et al., 2013; Wang et al., 2017).

Biodiversity is now widely recognized as the main driver of ecosystem functions, but in practice, the relationship between plant diversity and ESs is extremely complex (Alcamo et al., 2003; Hooper et al., 2005; Bullock et al., 2011; Turner et al., 2011; Harrison et al., 2014; Duncan et al., 2015; van der Plas et al., 2016). The effects and relative importance of plant diversity often vary with the ES indicators, spatio-temporal scales and assessment methods used (Quijas et al., 2012; Ricketts et al., 2016). For example, provisioning services tend to depend more strongly on specific tree species or functional groups than on plant diversity, whereas regulation and maintenance services tend to be largely influenced by overall plant diversity (Cardinale et al., 2012; Quijas et al., 2012; Harrison et al., 2014; Ricketts et al., 2016). The species diversity of a community and the diversity of communities within a landscape are important in the context of ES maintenance and delivery (Quijas et al., 2012). That is, the individual contribution of different tree species or communities to ESs likely differs, yet in some studies has simultaneously been considered in syntheses (Balvanera et al., 2006; Luck et al., 2009; Quijas et al., 2010; Quijas et al., 2012; Galicia and Zarco-Arista, 2014). As one of the world's recognized biodiversity hotspots, subtropical China is characterized by humid and warm monsoon climatic conditions in which diverse tree species thrive (Yu et al., 2014; Xiang et al., 2016). Depending on the intensity of human disturbances, subtropical secondary forests can be generally categorized into coniferous, deciduous broadleaved, and evergreen broadleaved forests along predictable restoration gradients (Yu et al., 2014; Ouyang et al., 2016; Xiang et al., 2016). The relatively high diversity of tree species in these forests compared with other forests at the same latitude providing an ideal research setting in which to analyze the influences of plant diversity and tree functional groups on ESs and associated trade-offs.

The Common International Classification of Ecosystem Services (CICES) has been used widely for designing indicators, mapping, and valuation in ESs research (Haines-Young and Potschin, 2018). Here, we used the CICES framework (v5.1) for indicator selection to study ESs and their trade-offs in subtropical forests in southern China at contrasting succession stages of restoration. Because it is difficult to directly measure multiple ecosystem indicators, previous studies typically relied on remotely sensed and modeled data of landscape characteristics as proxies for quantifying ESs (Egoh et al., 2008; Raudsepp-Hearne et al., 2010; Alamgir et al., 2016; Yu and Han, 2016). While these proxies—such as area, land use, and land cover—are useful for rapidly measuring ESs at coarse scales, they lack sufficient precision to analyze tree specie's impact on ESs and their interactions at fine scales because their relationships to ESs remain largely untested (Bennett et al., 2009; Burkhard et al., 2012; Quijas et al., 2012; Alamgir et al., 2016; Wang et al., 2017). Therefore, here we used field-based indicators from data measured in 100 subplots (1 ha in total) in each of three forests corresponding to a restoration stage. This should capture and represent ESs more consistently than do other indirect proxies (Alamgir et al., 2016). Our study objectives were to: (1) investigate how ES indicators and benefits varied with the stage of secondary forest restoration; (2) quantify the trade-offs between paired ESs and analyze the variation in specific trade-offs as they changed along the restoration gradient; and (3) examine the influence of plant diversity and functional groups (conifer, deciduous broadleaf, and evergreen broadleaf) on trade-offs among ESs.

2. Materials and methods

2.1. Overview of the study site

This research was carried out in the Dashanchong Forest Park (28°24′N, 113°18′E) in Changsha County, Hunan Province, China (Fig. 1). Here the elevation ranges from 55—260 m a.s.l. and the soil type is well-drained clay loam red soil (Alliti-Udic Ferrosols) developed from slate parent rock. The climate in this region is humid mid-subtropical monsoon, having an average annual precipitation of 1416.4 mm that mainly comes between April and August, and an average annual temperature of 16.6–17.6 °C; highest and lowest monthly average temperatures occur in July (39.8 °C) and January (−10.3 °C), respectively (Zeng et al., 2017). Owing to these favorable climatic conditions, the zonal vegetation is evergreen broadleaved forest dominated by *Fagaceae*, *Lauraceae*, *Magnoliaceae* and *Elaeocarpaceae* tree species. However, most of the primary evergreen broadleaved forests were damaged or destroyed to a large extent by human disturbance until the late 1950s; since then secondary forest vegetation has developed (Ouyang et al., 2016). Dashanchong Forest Park was established to guarantee the natural course of restoration in this region, its main objective being to conserve biodiversity and improve ecosystem services provided by subtropical forests. The dominant species here are native local trees, namely *Cyclobalanopsis glauca*, *Lithocarpus glaber*, *Choerospondias axillaris*, *Symplocos setchuensis*, and *Cleyera japonica*. We selected three types of secondary forest that represented the early, mid, and late stages of its restoration. These were respectively characterized as *Pinus massoniana–L. glaber* conifer broadleaf (PM), *C. axillaris* deciduous (CA) and *C. glauca–L. glaber* evergreen broadleaf forest (LG). All three forests had a closed canopy structure and a well-developed litter layer (Zeng et al., 2017).

2.2. Sampling design

In each of the tree forests, a 1-ha permanent plot was established and divided into 10-m × 10-m subplots to map the locations of

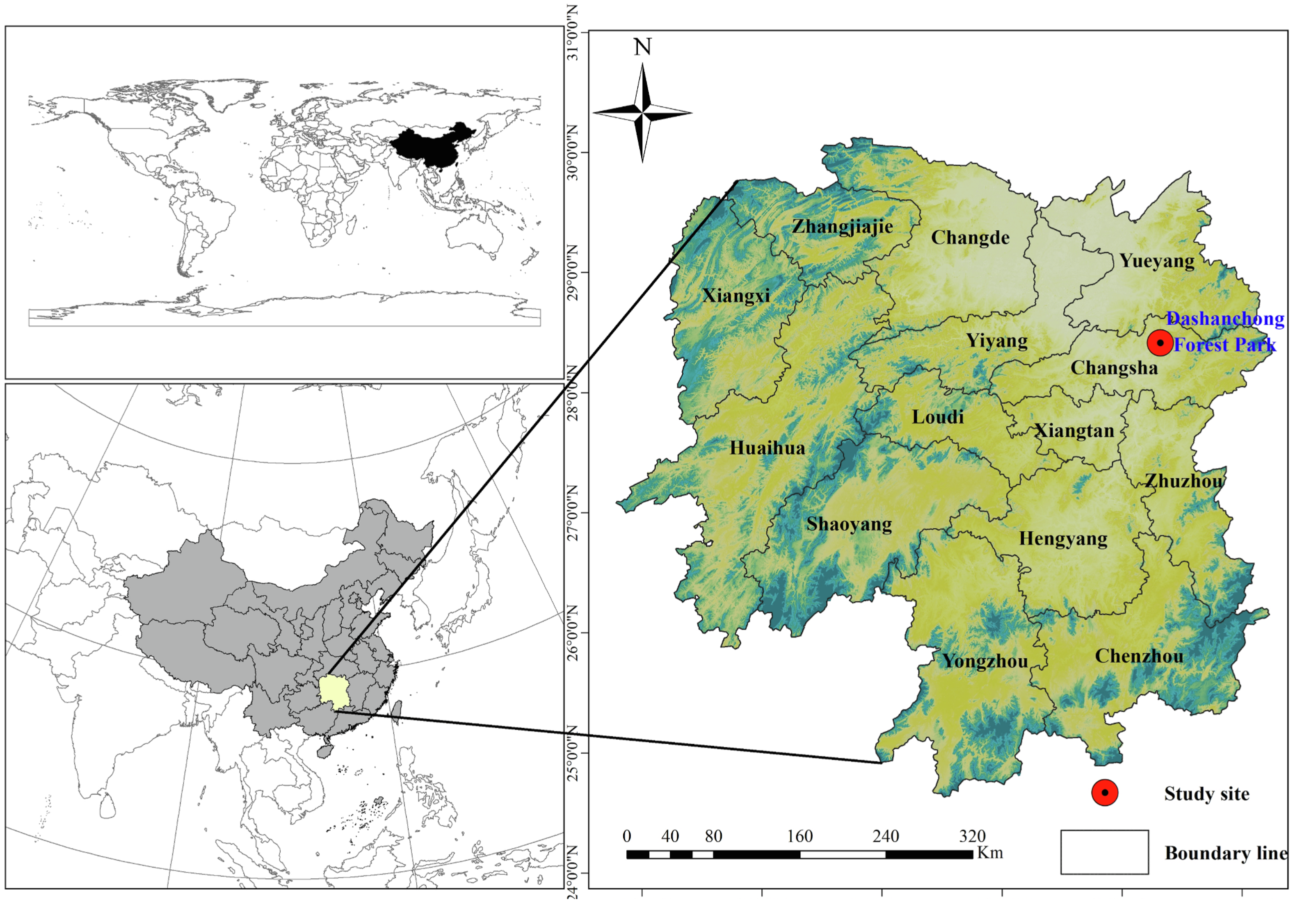

Fig. 1. Location of the Dashanchong Forest Park.

Table 1
Characteristics of the three secondary forests undergoing restoration that were studied in the Dashanchong Forest Park, China.

Restoration stage	Functional group composition (%)		Dominant species	IVI (%)	Average DBH (cm)	Average height (m)
Early	Conifer	57.21	*Pinus massoniana*	28.24	14.4	12.5
(PM)	Deciduous broadleaved	19.01	*Lithocarpus glaber*	20.04	7.2	7.4
	Evergreen broadleaved	23.73	*Cinnamomum bodinieri*	10.64	15.1	10.8
			Cyclobalanopsis glauca	7.51	10.3	7.8
			Liquidambar formosana	6.34	13.4	10.1
Mid	Conifer	0.05	*Choerospondias axillaris*	26.49	23.3	15.7
(CA)	Deciduous broadleaved	80.99	*Loropetalum chinense*	15.51	5.2	4.9
	Evergreen broadleaved	15.96	*Symplocos setchuensis*	6.72	6.4	5.2
			Vernicia montana	4.99	10.4	9.7
			Vernicia fordii	3.91	11.4	10.0
Late	Conifer	20.42	*Lithocarpus glaber*	25.93	10.4	9.6
(LG)	Deciduous broadleaved	39.81	*Cyclobalanopsis glauca*	9.90	12.8	10.4
	Evergreen broadleaved	38.79	*Pinus massoniana*	9.77	18.0	14.2
			Choerospondias axillaris	7.91	19.3	13.5
			Cleyera japonica	7.42	5.9	5.8

PM, *Pinus massoniana–Lithocarpus glaber* conifer broadleaved forest; CA, *Choerospondias axillaris* forest; LG, *Cyclobalanopsis glauca–L. glaber* evergreen broadleaved forest; DBH, diameter at breast height. IVI, important value index: IVI = sum of (RF + RD + RDo)/3, where RF, RD, and RDo are respectively the relative frequency, relative density, and relative dominance.

individual plants (DBH ≥ 1 cm), including trees, shrubs, and woody vines, and to record their species identity, diameter at breast height (DBH, at 1.3 m), height, and crown width of each stem (Zeng et al., 2017). The overall plant category and life-form composition of the three restoration forests is given in Table S1. As expected, herbaceous plants were relatively rare because of the closed canopy in these secondary forests. All the plants with DBH ≥ 1 cm were used to calculate the Shannon-Wiener biodiversity index for each of the three investigated forests (Condit, 1977). Their dominant tree species compositions and characteristics are in Table 1. Tables S2–S4 provide further details on the composition and quantitative characteristics of the top 10 species (DBH ≥ 4 cm) in each forest.

2.3. Quantification of plant diversity and ESs

We quantified plant diversity and four ES indicators: air quality regulation, maintenance of soil fertility, global climate regulation, and timber provision (Table 2). These ESs are consistent with several studies in which they were deemed critical to forest restoration as well as human welfare (Alamgir et al., 2016; Lu et al., 2014; Onaindia et al., 2013).

Table 2
The attributes and quantified indicators of plant diversity and ESs in this study.

	Attribute	Indicator
Plant diversity	Higher plant diversity implies greater insurance that an ecosystem will provide higher and more predictable services	Shannon-Wiener diversity index
Regulation and maintenance services:		
Air quality regulation	Forest plays an important role in the mitigation of air pollution	Leaf area index (LAI)
Maintenance of soil fertility	Key indicator of soil quality and the capacity of soil to carry out nutrient cycling	Soil organic carbon storage (SOCS) ($t \cdot ha^{-1}$); Total nitrogen storage (TNS) ($t \cdot ha^{-1}$)
Global climate regulation	Global climate regulation via reduction of greenhouse gas concentrations	Sequestered atmospheric CO_2 by total tree biomass (CO_2 equ. $Mg \cdot ha^{-1}$)
Provisioning services:		
Timber	The presence of tree species with potential use for timber	Basal area (BA) ($m^2 \cdot ha^{-1}$)

2.3.1. Plant diversity

The Shannon-Wiener diversity index (H') was used as a metric of plant diversity:

$$H' = -\sum_{i=1}^{s} P_i \ln P_i.$$

where s is the total number of species present in a subplot and, P_i is the proportion of the importance values of species i to all species (Lu et al., 2014).

2.3.2. Air quality regulation

Since plant photosynthesis and respiration processes predominantly take place in trees' leave, the potential for air purification may be estimated from the extent of their leaf coverage by using LAI (Bottalico et al., 2017; Manes et al., 2016). This was defined as the total leaf area of one side of a leaf per unit ground surface area. We measured LAI using hemispherical photographs taken at 1 m above ground level in each subplot with a LAI measuring instrument (SY-S01A, Shiya Technology Inc., Hebei, China) in spring (April), summer (July), and autumn (October) in 2014, and in winter (January) 2015 (Zhu et al., 2016). Photographs were taken in the morning, at dusk, or in cloudy conditions to minimize the influence of direct sunshine (Zhu et al., 2016). Plant canopy analysis software (from the instrument's manufacturer) was used to process the images and calculate the mean value of LAIs in the four seasons.

2.3.3. Maintenance of soil fertility

We collected two cylindrical soil core samples, 10 cm apart, from the top 30 cm soil layer in each subplot, to analyze soil moisture and SOC content and TN concentration as indicators of nutrient cycling and energy flows. The SOC concentrations at depths of 0–10 cm, 10–20 cm, and 20–30 cm were measured by the wet combustion method using the oxidization of potassium bichromate (Zeng et al., 2017). Soil TN concentrations at the three depths were measured using the Semimicro-Kjeldahl method, whereby TN was digested with a mixture of H_2SO_4, K_2SO_4, $CuSO_4$, and Se (Xiang et al., 2009). Soil organic carbon storage (SOCS) and total nitrogen storage (TNS) ($t \cdot ha^{-1}$) were estimated using these two equations (following Zhang et al., 2013):

$$SOCS = \frac{1}{10} \cdot \sum_{i=1}^{n} SOC_i \times B_i \times H_i \times (1 - G_i)$$

$$TNS = \frac{1}{10} \cdot \sum_{i=1}^{n} TN_i \times B_i \times H_i \times (1 - G_i)$$

where SOC_i is the SOC content ($g \cdot kg^{-1}$), TN_i is the soil TN content ($g \cdot kg^{-1}$), B_i is the soil bulk density ($g \cdot cm^{-3}$), H_i is the soil sampling thickness (cm), G_i is the fraction of gravel (%) at depth i.

2.3.4. Global climate regulation

Forest biomass has great potential for reducing carbon (C) emissions and mitigating pollution (McKinley et al., 2011; Xiang et al., 2016). The sequestered CO_2 equivalent (CO_2 equ $Mg \cdot ha^{-1}$) was estimated with this equation (Alamgir et al., 2016):

$$CO_2 equ. = W \times 0.50 \times 3.67$$

where W is tree biomass, estimated as the total biomass of stem, branch, leaf, and root material of each tree using species-specific and general algometric equations wherein DBH (D) was the predictor (Xiang et al., 2016). The constant 0.50 is the conversion coefficient of tree biomass into biomass carbon storage. The constant 3.67 is the conversion coefficient of carbon storage into CO_2 equ (IPCC, 2006; Feng et al., 2017).

2.3.5. Timber provisioning

Timber production ($m^2 \cdot ha^{-1}$) was estimated as BA, wherein D is DBH:

$$BA = \pi \times D^2/4$$

2.4. Calculation of trade-offs

The trade-offs between two ESs reflected their direct interactions, whereas among multiple ESs were more complex to understand (Lu et al., 2014). Therefore, we tested trade-offs among 15 combinations of paired ESs (including between plant diversity and four ESs). Root mean square deviation (RMSD) is a commonly used statistical parameter to measure the magnitude of trade-offs among the ESs (Lu et al., 2014; Feng et al., 2017). Following Bradford and D'Amato (2012), before calculating the RMSD, the benefit from every ES was first standardized to eliminate units differences among ESs, as follows:

$$ES_{std} = \frac{ES_{obs} - ES_{min}}{ES_{max} - ES_{min}}$$

where ES_{std} is the standardized value (0–1) of a given ES; ES_{obs} is the observed value; and ES_{max} and ES_{min} are the maximum and minimum observed values, respectively. Then, the RMSD (Bradford and D'Amato, 2012; Feng et al., 2017) was calculated as:

$$RMSD = \sqrt{\frac{1}{n-1} \cdot \sum_{i=1}^{n} (ES_i - ES_{exp})^2}$$

where ES_i is the standardized value of ES_i and ES_{exp} is the expected value of the ith number of ESs. Thus, in comparing the magnitude of trade-offs between any two ESs, their RMSD value represents the departure from the 1:1 line of equal benefit. The larger angle with the vertical axis than that with the horizontal axis indicates more beneficial for the ES represented by the horizontal axis, and vice versa. Meanwhile, the larger the angle between spikes and the 1:1 line, the higher the trade-offs between the paired ESs if the lengths of spikes are the same.

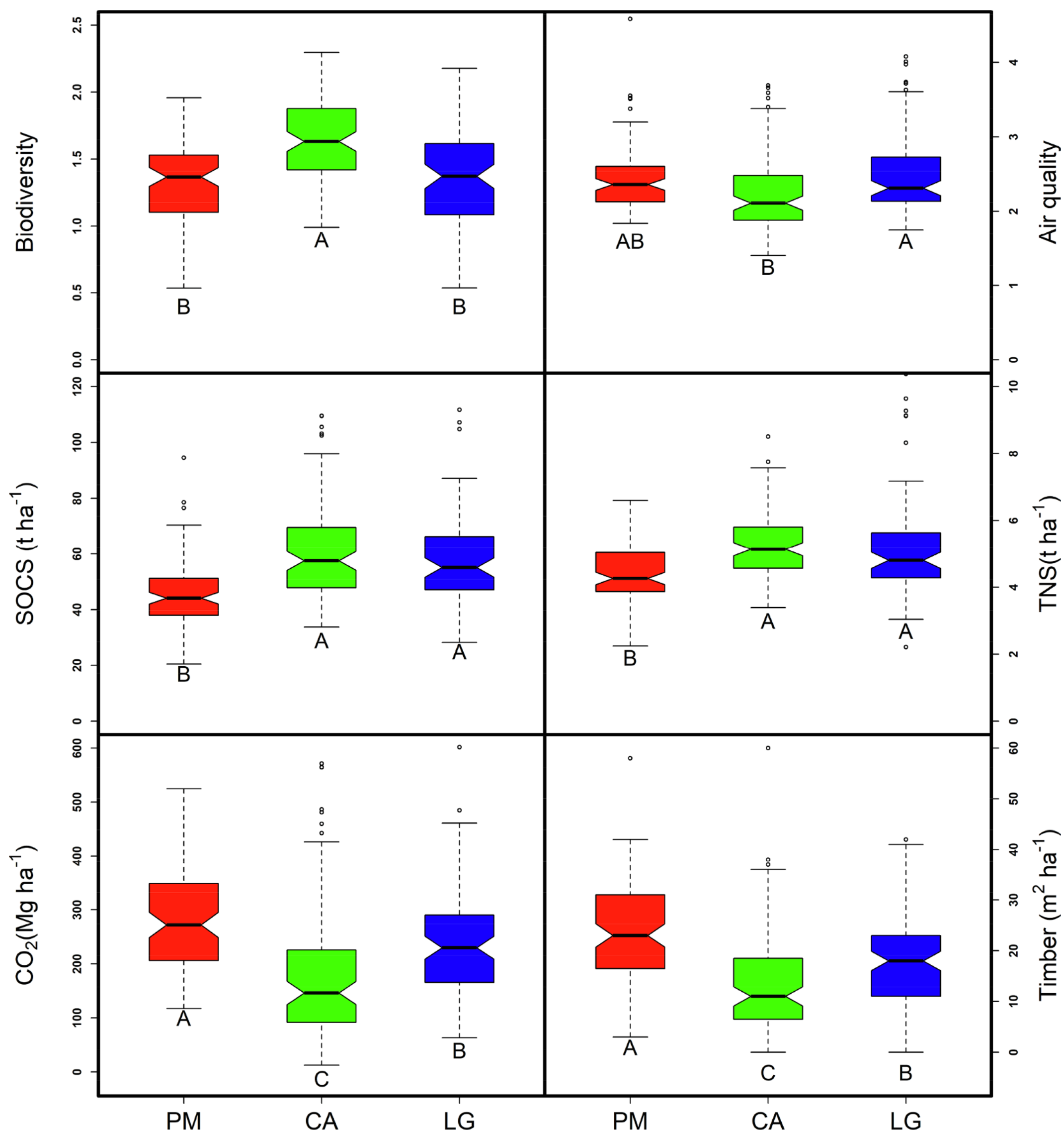

Fig. 2. Comparison of plant diversity and ESs among the three secondary forests along a restoration gradient. PM: early stage forest; CA: mid stage forest; LG: late stage forest. For a given variable, different capital letters (A, B and C) beneath each boxplot indicate significant differences ($p < 0.05$) between the forests.

2.5. Statistical analysis

One-way ANOVA was used to test for differences in the respective benefits of ESs and their trade-offs among the three forest restoration stages. Correlations between proportions of coniferous, deciduous broadleaf, and evergreen broadleaf tree species, and between trade-offs of paired ESs, were tested using the Pearson correlation coefficient. To conduct the statistical analysis, and draw plots, we used the R v3.3.1 software platform.

3. Results

3.1. Quantification of plant diversity and ESs

Fig. 2 shows the obtained plant diversity and multiple ESs in different units. Ecological indicators differed among the three restoration forests, where plant diversity was greatest in the mid stage forest (CA), but air quality and global climate regulation, and timber provisioning were lowest. SOCS and TNS were higher in the mid and the late (LG) stage forests than in the early stage (PM). Global climate regulation and timber provisioning were greatest in the early stage forest.

3.2. Relative benefits of plant diversity and ESs

We used flower diagrams (Fig. 3) to show the relative benefit (standardized ES value) of plant diversity and multiple ESs in each of the three forests. The outer edge of the flower petals conveys the relative contribution of an individual indicator in a specific forest. When pooled, their relative benefits ranged from 0.2 to 0.6. Hence, we defined values > 0.4 as conferring "high benefit", those between 0.3 and 0.4 as "moderate benefit", < 0.3 as "low benefit". Clearly, the pattern of these relative benefits varied among the three restoration secondary forests; however, biodiversity consistently elicited the greatest and highest (i.e., > 0.4) relative benefit. The early stage forest (PM) provided low benefit level of TNS, global climate and air quality regulation, and moderate benefit level of SOCS regulation and timber provisioning. The mid stage forest (CA) provided low benefit lever of timber production, global climate and air quality regulation, and moderate benefit level of soil nutrient storage (SOCS and TNS) regulation. The late stage forest (LG) provided high benefit level of timber provisioning, and moderate benefit level of TNS, global climate and air quality regulation, and low benefit level of SOCS regulation.

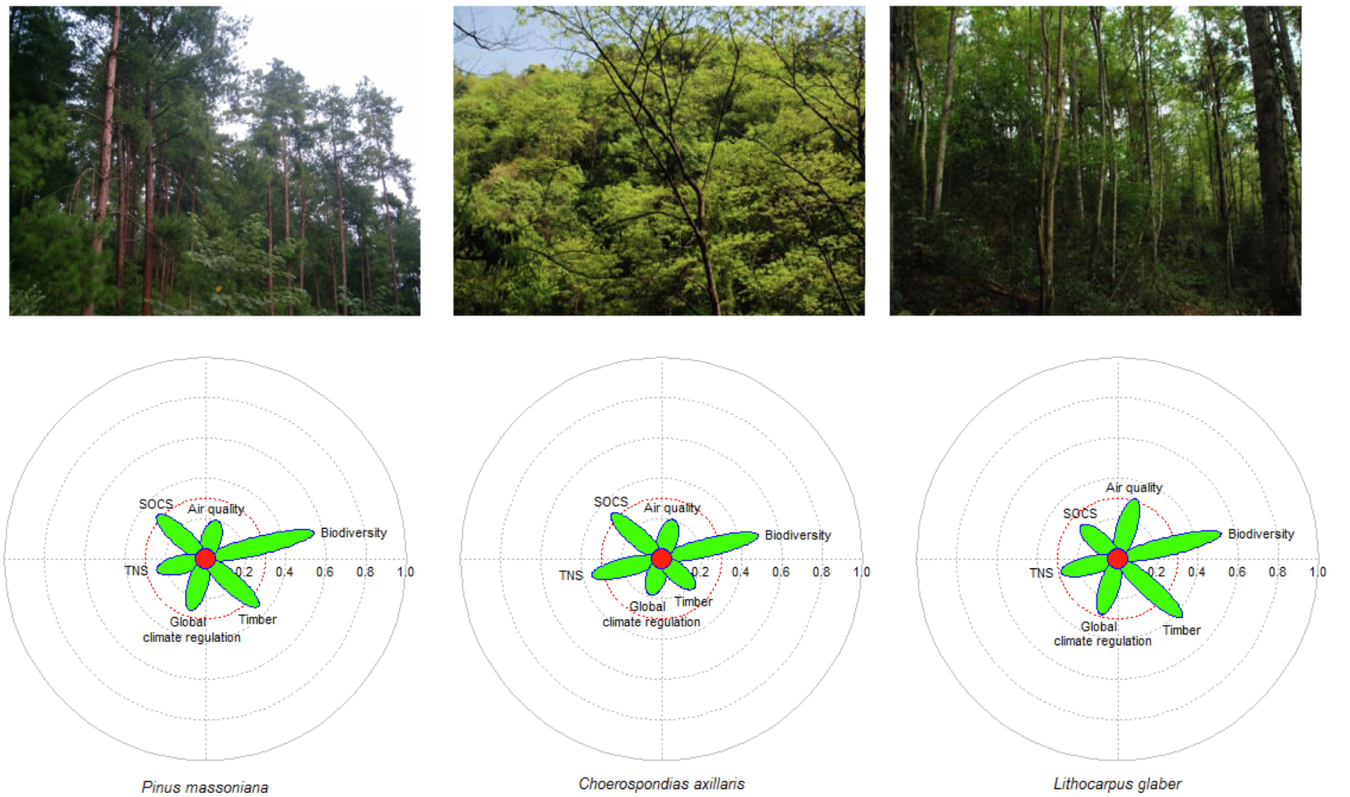

Fig. 3. Flower diagrams of the relative benefits of plant diversity and ESs in the restoration forests. Each flower represents the plant diversity and multiple ESs for one secondary forest. *Pinus massoniana*: early stage forest; *Choerospondias axillaris*: mid stage forest; *Lithocarpus glaber*: late stage forest.

3.3. Trade-offs between ecological indicators

Fig. 4 shows scatter plots of paired ESs, in which the spikes are drawn from the origin. Trade-offs between ESs and the beneficiary of the same paired trade-offs differed and varied among the three forests. For example, trade-offs between TNS and global climate regulation, and between TNS and timber provisioning, favored global climate regulation and timber provision in the early (PM) and late (LG) stage forests but instead favored TNS in the mid stage forest (CA).

The average magnitude of trade-offs between paired ecological indicators was defined as high for an RMSD > 0.2, low or synergistic when RMSD was < 0.1, and moderate when RMSD was between 0.1 and 0.2. We found high degrees of trade-offs between plant diversity and the ESs in all three forests, and those in the late stage forest (LG) between timber and air quality, SOCS and TNS, respectively (Table 3). Low levels of trade-offs or synergy were found between SOCS and TNS in the three forest types. The trade-offs in other paired ESs were moderate and significantly different among forests, except for that between air quality and SOCS. Generally, the magnitudes of trade-offs in late stage (LG) forest exceeded those of the other two forests. Specifically, trade-offs for the pairs of air and TNS, air and global climate, air and timber, SOCS and timber, and TNS and timber were significantly higher in LG than one or both other forests. Trade-offs between soil nutrient storage (SOCS and TNS) and global climate regulation were higher in the mid stage forest (CA) than in the early stage forest (PM). We also detected higher levels of trade-offs between global climate regulation and timber provisioning in the early stage forest (PM) than in the other two forests.

3.4. Effects of tree functional group on trade-offs between plant diversity and ESs

We found that the tree functional group influenced trade-offs between plant diversity and air quality regulation, global climate regulation, and timber provision significantly (Table 4). To be specific, deciduous broadleaf tree species positively influenced the above-mentioned trade-offs, whereas the conifer and evergreen broadleaf tree species negatively influenced them.

4. Discussion

4.1. Effects of forest restoration on ES indicators and benefits

We found that in the late stage of secondary forest restoration, the overall benefits of assessed ESs were the highest among the three forests. In particular, individual ES benefits tended to be more evenly distributed in the high and moderate classes, indicating that late stage forest was a better provider of multiple ESs. These results are consistent with those from studies of restored forest ecosystems on agricultural land, where it was suggested interactions among environmental heterogeneity, disturbance, habitat fragmentation, and seed dispersal processes were responsible for enhanced ESs (Benayas et al., 2009; Benayas and Bullock, 2012). It is likely that forests in late stages of restoration feature greater potential than those at the early or mid stages for providing long-term ecological benefits and economic profits at higher levels (Bennett et al., 2009; Bradford and D'Amato, 2012).

Yet variation in the quantified individual ESs did not show a consistent pattern along the restoration gradient. For example, plant diversity was greatest in the mid stage forest, in line with Odum's theory that it increases but then declines along a successional gradient (Odum, 1969). The early stage forest offered higher levels of global climate regulation and timber provisioning ESs. This result could be explained by faster growth rates of its dominant pioneer tree species, *P. massoniana* (Onaindia et al., 2013; Zeng et al., 2017).

4.2. Effects of forest restoration on trade-offs between paired ESs

It is widely accepted that trade-offs exist between multiple ESs,

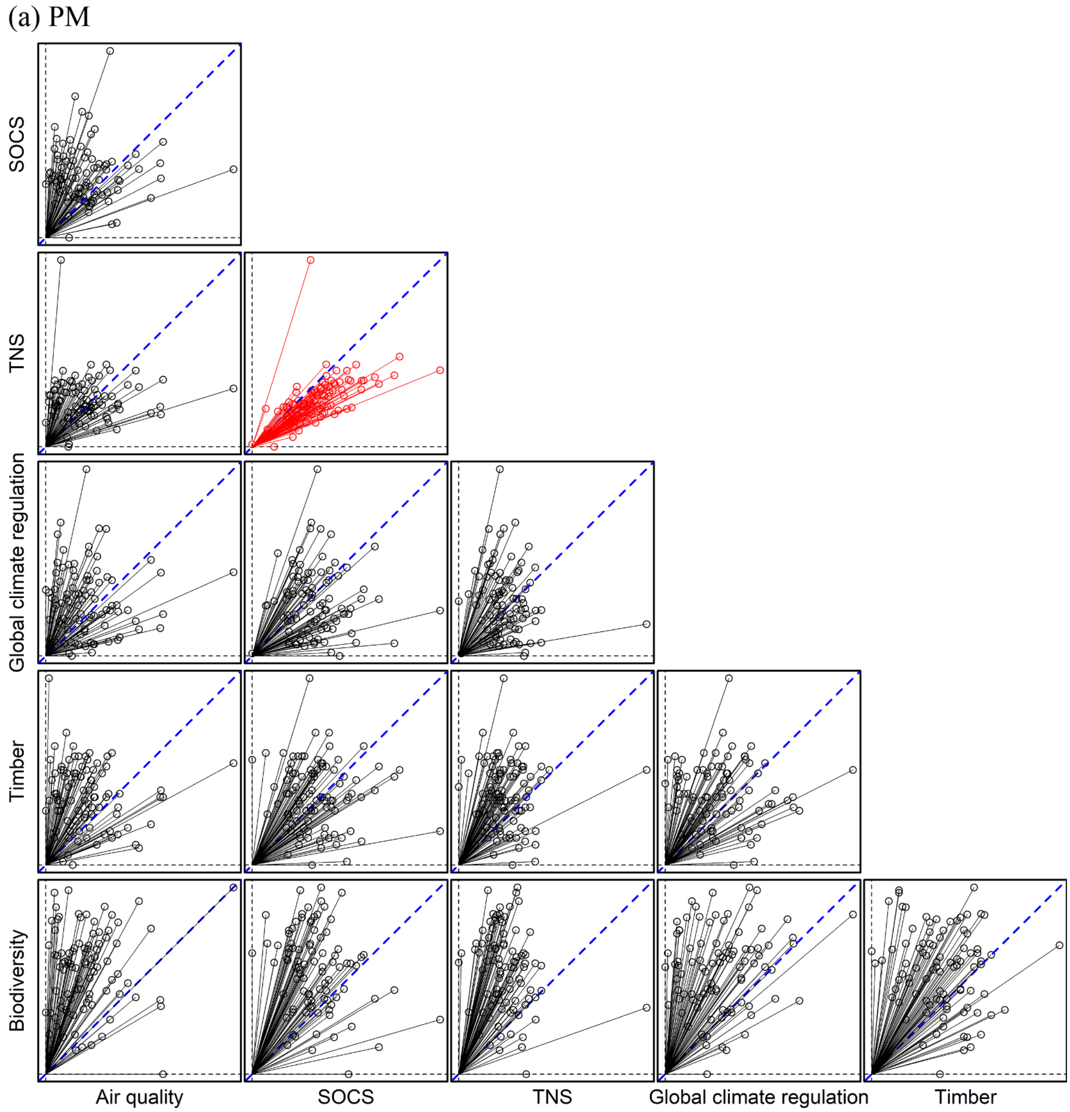

Fig. 4. Scatter-plot matrices of paired ecological indicators (standardized values) from the three secondary forests. PM: early stage forest; CA: mid stage forest; LG: late stage forest. Scatter-plots in red indicate that the beneficiary in the paired trade-off differed from the other two forests.

especially among provision ESs, but also for provision and regulating ESs, and biological diversity as well as other types of ES (Bennett et al., 2009; Carpenter et al., 2009; Alamgir et al., 2016; Wang et al., 2017). Low degrees of trade-off or synergy were only found to occur between SOCS and TNS in each of the three forests, thus supporting findings from previous studies (Yang et al., 2011; Lu et al., 2014). While trade-offs among ESs have been researched extensively in different forests and regions, few have tried to analyze the variation in one or several specific trade-offs as they changed from one forest to another forest (Dickie et al., 2011; Maskell et al., 2013; Wang et al., 2017). Here, we investigated how trade-offs between paired ESs varied with different secondary forest types. We found that not only the magnitudes but also the beneficiary changed along the restoration gradient.

In general, the magnitude of ES trade-offs was the greatest in the late stage forest, namely between air quality regulation and other ESs (TNS, global climate regulation and timber provisioning), as well as between timber provisioning and maintenance of soil fertility. These results reflect the stronger interspecific competition for light in a denser canopy in late stage evergreen broadleaf forest, and the competition between trunk growth and soil nutrient concentrations (Alamgir et al., 2016). Moreover, we found that the beneficiary in several paired trade-offs changed along the restoration gradient, and these patterns corresponded to variation in the relative contribution of an individual ES. Trade-offs between two regulating ESs, air quality and SOCS, changed from favoring SOCS in the early and mid stage forests to favoring air quality in the late stage forest. Likewise, trade-offs between the SOCS and the global climate regulation, and between the timber provisioning favored SOCS in the early and mid stage forests, whereas global climate regulation and timber provisioning were favored in the late restoration forest. These results reflect the highest contributions of air quality, global climate regulation and timber provisioning, as well as the lowest contribution of SOCS in the late stage forest. A reverse pattern of variation between the maintenance of soil fertility ES (TNS) and global climate regulation and the timber provisioning ESs was found in the mid stage forest, where trade-offs shifted from favoring timber and global climate regulation in the early and late stage forests to TNS in the mid stage forest. These results may reflect the highest level of TNS and the lowest levels of timber provisioning and global climate regulation in the mid stage forest. Although the trade-off values between SOCS and TNS were as low as can be considered as synergy, the beneficiary changed from TNS in the mid and late stage forests to SOCS in the early stage forest, and this could well explain the lowest level of TNS in early stage forest. Feng et al. (2017) also noted that changes in ES trade-offs were more complex than in benefits of ESs in a

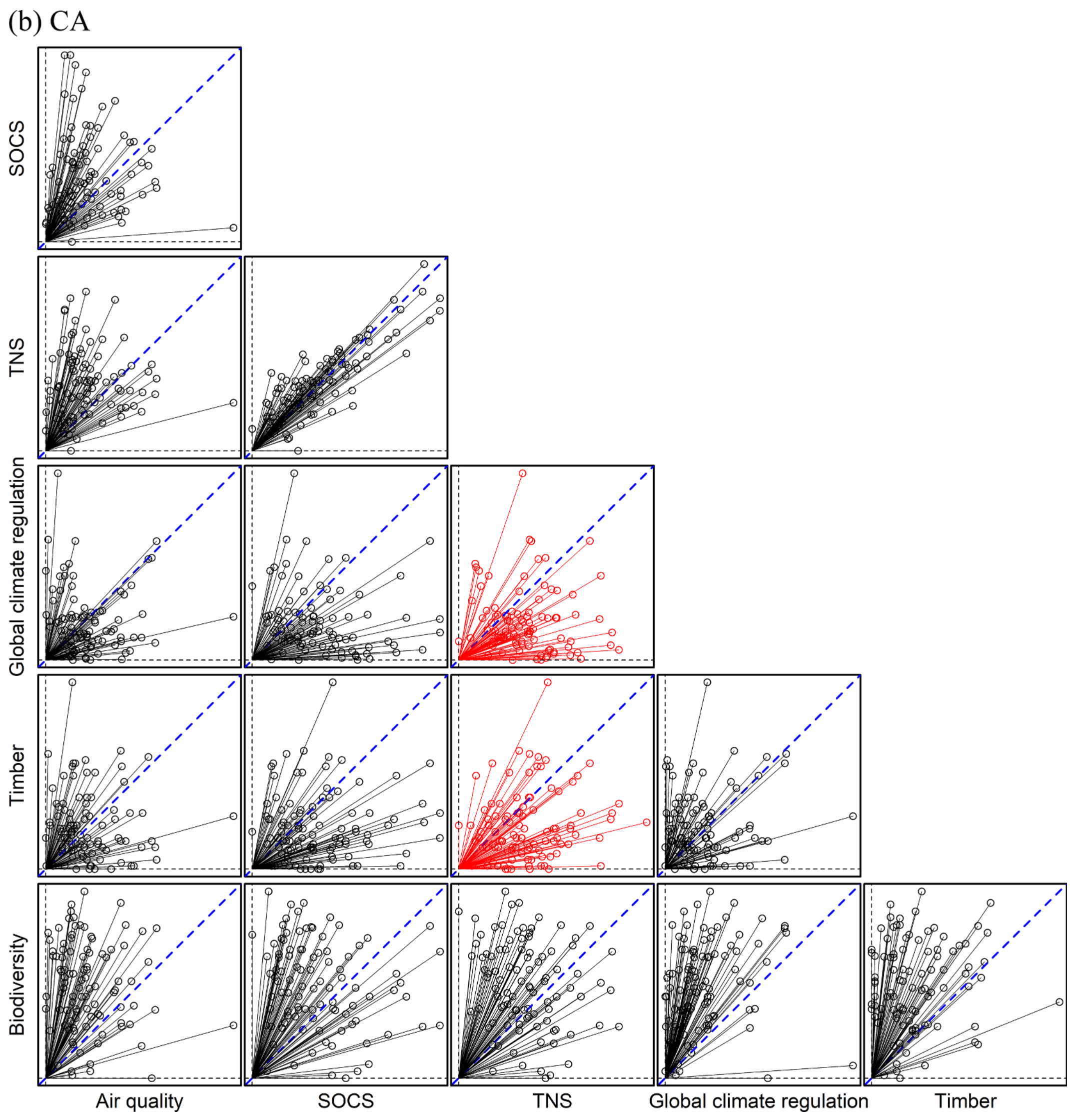

Fig. 4. (*continued*)

study on the Loess Plateau of China. Besides the effect of complex relationships among ESs, we should also consider the magnitude of their variation in addition to shifted beneficiary in trade-offs across different forests. Moreover, precisely because multiple trade-offs may involve the same ES, with some trade-offs more pronounced than others, it seems necessary to combine multiple ES trade-offs and their variation patterns for ES prediction and management. Doing this could also provide a novel approach for better understanding the complexity of ES variability (Howe et al., 2014; Feng et al., 2017).

4.3. Effects of plant diversity and tree functional groups on ES trade-offs

Since plants participate in all ecological processes, such as photosynthesis and nutrient cycling, complex relationships exist between plant diversity and ESs (Quijas et al., 2012; Lu et al., 2014; Ricketts et al., 2016). In our study, plant diversity peaked in the mid stage forest, alongside the highest levels of maintenance of soil fertility, yet lowest levels of global climate regulation and timber provisioning. These results are consistent with the view that some regulating ESs, such as soil processes, likely increase with plant diversity, whereas provisioning ESs (e.g., timber production), depend on harvestable species' abundance (e.g., *P. massoniana* here) and may be independent of biodiversity (Cardinale et al., 2012; Ricketts et al., 2016).

We consistently found that trade-offs involving plant diversity were the strongest of all ESs, as has been reported elsewhere (Lu et al., 2014). Our results showed the tree functional group significantly influenced plant diversity-relevant trade-offs. Deciduous broadleaf tree species positively influenced several plant diversity-relevant trade-offs, whereas conifer and evergreen broadleaf tree species negatively influenced them. A possible reason for this is that the growth and turnover of leaves in deciduous forest sustains less standing biomass, less canopy cover, and more forest disturbance. This likely reduces the capacity for provision of multiple ESs; that is, the magnitudes of trade-offs between increased deciduous diversity and other ESs become stronger (Liddell et al., 2007; Silk et al., 2013; Alamgir et al., 2016). In sum, that tree functional group compositions changed during forest restoration is a major factor influencing the trade-offs between ESs, and thus their respective benefits.

4.4. Limitations of this study

Consistent with many previous papers on ESs, we used the method of Bradford and D'Amato (2012) to quantify the individual benefit of ESs and the trade-offs among them (Lu et al., 2014; Feng et al., 2017). This approach relying on simple statistical measures is user-friendly and promising for various management options and objectives (Bradford and D'Amato, 2012). In our study, there were 100 subplots sampled per forests, presumably making the analysis more precise, yet also more

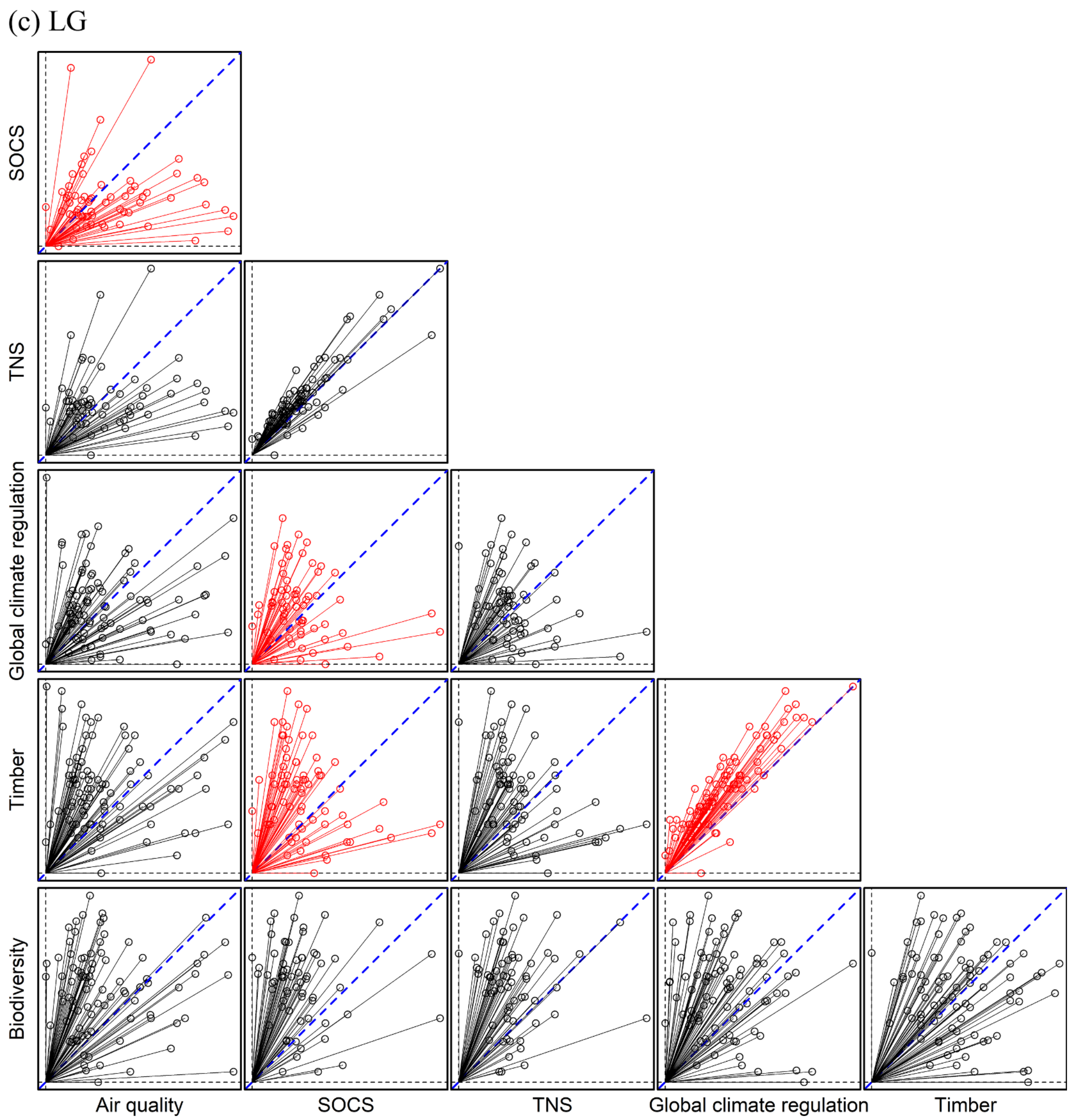

Fig. 4. (*continued*)

Table 3
Root mean square deviation (RMSD) values of the paired trade-offs among three secondary forests undergoing restoration in the Dashanchong Forest Park, China. PM: early stage forest; CA: mid stage forest; LG: late stage forest. Different lower case letters indicate significant differences ($p < 0.05$) in the magnitude of trade-offs between forests. Higher-degree of trade-offs are highlighted in darker shades of gray.

Restoration stages	Paired ES trade-offs	SOCS	TNS	Global climate regulation	Timber	Biodiversity
PM	Air quality	0.14±0.11	0.10±0.10[b]	0.14±0.11[ab]	0.17±0.12[a]	0.26±0.15[a]
CA		0.16±0.14	0.15±0.12[a]	0.12±0.12[b]	0.13±0.11[b]	0.24±0.16[ab]
LG		0.15±0.15	0.15±0.14[a]	0.16±0.14[a]	0.20±0.15[a]	0.21±0.15[b]
PM	SOCS		0.09±0.08	0.13±0.11[b]	0.13±0.11[c]	0.21±0.15
CA			0.06±0.05	0.18±0.15[a]	0.17±0.13[b]	0.23±0.15
LG			0.05±0.04	0.15±0.12[ab]	0.21±0.14[a]	0.24±0.14
PM	TNS			0.13±0.11[b]	0.14±0.10[b]	0.24±0.15[a]
CA				0.17±0.13[a]	0.16±0.12[b]	0.20±0.14[b]
LG				0.15±0.13[ab]	0.20±0.15[a]	0.21±0.14[ab]
PM	Climate regulation				0.16±0.10[a]	0.22±0.15
CA					0.13±0.11[b]	0.23±0.15
LG					0.10±0.05[b]	0.20±0.15
PM	Timber					0.20±0.14
CA						0.23±0.16
LG						0.19±0.14

Table 4
Effects of tree functional groups on trade-offs between plant diversity and ESs in secondary forests at three restoration stages.

Restoration stage	ESs	Functional group composition (%)		
		Conifer	Deciduous broadleaf	Evergreen broadleaf
Early (PM)	Plant diversity—Air quality	-0.22^{*}		
	Plant diversity—Timber	-0.31^{**}	0.27^{**}	
Mid (CA)	Plant diversity—Timber		0.29^{**}	-0.33^{**}
Late (LG)	Plant diversity—Air quality	-0.26^{*}	0.38^{**}	-0.23^{*}
	Plant diversity—Global climate regulation		0.31^{**}	-0.24^{*}
	Plant diversity—Timber		0.27^{*}	-0.31^{**}

PM, *Pinus massoniana–Lithocarpus glaber* conifer broadleaved forest; CA, *Choerospondias axillaris* forest; LG, *Cyclobalanopsis glauca–L. glaber* evergreen broadleaved forest. Asterisks indicate significant differences at $^{*}p < 0.05$, and $^{**}p < 0.01$.

labor intensive. Therefore, one limitation is that we could not investigate ESs and trade-offs over time. Some ES indicators such as LAI depend on seasonal changes (phenology), and regulating ESs-relevant indicators, such as SOCS and TNS, usually change at slower rates than do provision services (Rodríguez et al., 2006; Zhu et al., 2016). Secondly, our results showed that the outcome of one specific ES depends on trade-offs in several pairs of ESs, considering some trade-offs more important than others. But to carry out a direct calculation and relationship analysis of trade-offs among three or more ESs is much more complicated and need more effective methods to evaluate them (Burkhard et al., 2012; Koschke et al., 2012). Additionally, though our selected ESs are critical to forest restoration and human welfare, other important indicators—such as soil water content, quantity and quality of ground and surface waters—should not be overlooked in future studies.

5. Conclusions

By measuring multiple ES indicators and quantifying trade-offs among them in three secondary forests, this study characterized the impact of forest restoration on the provision of ESs and the trade-offs among them. The results demonstrated that late stage forest could provide greater and more balanced ES benefits than those at the early and mid stages of restoration. Trade-offs between pairs of ESs changed not only in magnitude, but also in the beneficiary during the restoration process, especially the beneficiary shifting in one or two critical trade-offs were exactly corresponding to the tendency of specific ES value. Importantly, tree functional groups altered trade-offs between plant diversity and the ESs of air quality regulation, global climate regulation, and timber provisioning. The proportion of deciduous broadleaf trees positively impacted the trade-offs whereas coniferous and evergreen broadleaf trees negatively impacted them.

Although tree species in subtropical forests varied morphologically, they could be put into evergreen coniferous, deciduous broadleaved, and evergreen broadleaved functional groups. Hence, several recommendations for subtropical secondary forests management are suggested by our results. Moreover, the secondary forests are also viewed as templates for the sustainable management of mixed plantations and natural forests (Xiang et al., 2013; Ouyang et al., 2016). First, we suggest it is worthwhile to implement forest restoration because its late stage is more likely to provide greater long-term ecological benefits and economic sustainability. Second, we should seriously consider tree species composition in forest ES management, given their functional grouping influence on ES trade-offs, and also because the supply of timber provisioning ESs depends on specifically harvested tree species, such as *P. massoniana*. These results also imply that we can achieve diversified ecological outcomes in forests through the management of tree species composition. Third, land use in subtropical China has experienced rapid changes due to human activities and the implementation of ecological restoration projects. The evaluation and trade-off of ESs in forests at different restoration stages could provide valuable information for predicting the effects of land use changes on ES and land use planning.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.05.008.

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