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Review

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CForBio: a network monitoring Chinese forest biodiversity

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Abstract China harbors a rich variety of forest types and forest-associated biodiversity, linked to both historical and contemporary environmental factors. However, being a country with a large population and rapid economic development, its diverse forest is facing unprecedent challenges. The Chinese Forest Biodiversity Network (CForBio) was initiated 12 years ago to study the maintenance of biodiversity in China's forest ecosystems. In this review, we first summarize research progress in CForBio, and then give suggestions for future research. In the past 12 years, the research based on CForBio mainly focused on local ecological factors, such as environment filtering, biotic interactions and small-scale dispersal limitation. We suggest that future studies in CForBio should (1) continue research on trees, but expand more on insects, birds, mammals, microbes and other organism groups; (2) investigate the effects of widespread defaunation on forest biodiversity, structure and functioning; (3) evaluate the diverse effects of climate change on forest composition, structure and functioning; (4) include new technologies, such as remote sensing, to better monitor and study forest biodiversity change and maintenance.

Keywords Forest ecosystem · Defaunation · Climate change · Remote sensing

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1 Introduction

Forests play important roles in maintaining biodiversity and for the functioning of the biosphere [1, 2]. The majority of species described on Earth live in forests [1]. A recent study estimates that tropical forests may harbor about 40,000–53,000 tree species, most of which are extremely rare, indicating a high risk of extinction of these species [3]. Forests also account for a large proportion of gross primary production, plant biomass and carbon [4, 5].

Forests in China are especially unique in terms of the unbroken connections between tropical, subtropical, temperate and boreal forest [6, 7]. Although temperate forests in China, Europe and North America have similar species composition and community structure, China's temperate forests generally have higher taxonomic diversity and contain more unique paleoendemics than the other two regions [6, 8, 9]. Notably, all 10 biodiversity hotspots in China for both plants and animals, as well as the endemic and threatened component of them, are located in mountainous areas [10].

However, forests are now among the ecosystems that have been most severely affected by habitat destruction [7, 11]. Although overall area covered with forest is increasing in China, natural old-growth forests are still declining [12, 13]. China's large and still increasing human population as well as its rapid economic development is likely to have even stronger impacts on its forest biodiversity in the future decades. Therefore, China's forests are of critical importance for its biodiversity research and conservation in the future.

Chinese Forest Biodiversity Monitoring Network (CForBio, http://www.cfbiodiv.org), initiated in 2004, is aimed at monitoring the long-term biodiversity changes and investigating the mechanisms maintaining biodiversity, such as community assembly and species coexistence rules in China's forests. By 2014, this network included 13 large permanent forest plots, distributed across a latitudinal gradient, ranging from tropical forest in Xishuangbanna, Yunnan province, to a boreal coniferous forest at Daxinganling, Heilongjiang province, as shown in Fig. 1 [14]. Hundreds of papers on mechanisms underlying biodiversity patterns and forest community structure have been published from this network [14]. In this paper we will first summarize the progress made by CForBio, and then provide some suggestions for future research.

2 Research progresses made by CForBio

The assembly of biotic communities is shaped by both local factors, such as abiotic filtering, biotic interactions, anthropogenic impacts and local dispersal, as well as regional and historical factors, such as speciation, extinction, broad-scale migration and historical climate [15, 16]. We will introduce what has been learnt from CForBio on the roles of these factors in shaping the assembly of Chinese forest tree assemblages.

2.1 Local factors

Since the beginning of the era of community ecology in the 1950s, local interactions between species and environment or interactions among species have dominated in both theoretical and empirical studies of community ecology [17]. These interactions have also been a central topic in CForBio.

2.1.1 Habitat filtering

Habitat filtering has been widely reported to strongly shape species composition, functional and phylogenetic structure, producing a local clustered assembly of species with similar functional traits or close phylogenetic relations [18–21].

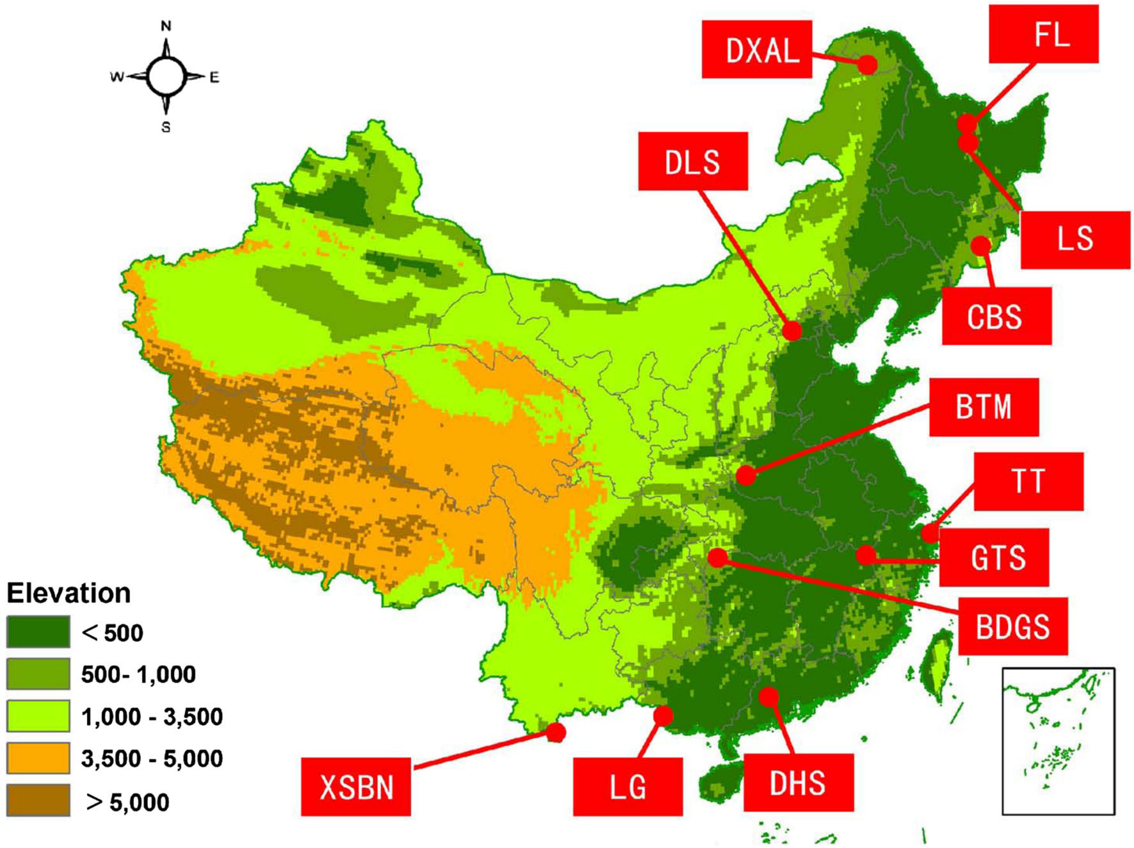

Fig. 1 Distribution of 13 large permanent forest plots across China. These plots are Daxing'anling (DXAL), Fenglin (FL), Liangshui (LS, two plots), Changbaishan (CBS), Donglingshan (DLS), Baotianman (BTM), Tiantong (TT), Gutianshan (GTS), Badagongshan (BDGS), Dinghushan (DHS), Longgang (LG), and Xishuangbanna (XSBN)

2.1.1.1 Topography Being an easily quantified synthetic proxy for many environmental resources such as soil moisture and nutrients as well as biotic conditions [22], the relations of topography to species diversity, composition and other aspects of community structure have been extensively studied [20, 21]. In Dinghushan (DHS) subtropical forest, the genetic structure of a dominant tree species (*Castanopsis chinensis*) is highly associated with the complex topography [23]. Strong species-topographic habitat associations are found in Gutianshan (GTS) subtropical forest [18]. Importantly, these associations may change across life stages, e.g., the associations can be consistent for saplings and juveniles, but change at mature stage [18]. Similar associations between dominant tree species and topography are also reported in Xishuangbanna (XSBN) tropical forest [24]. In addition, in the same forest, not only species diversity and composition, but also species traits show significant association with topography, i.e., higher elevations and steeper slopes having more species with slow growth and low turnover [21]. Lastly, community phylogenetic structure is also closely linked with topographic variables in DHS, with phylogenetic clustering in valley and low slope habitats, and phylogenetic overdispersion in high slope, ridge-top, and high gully habitats [20]. To sum up, topography has significantly affected the genetic structure, species composition, functional and phylogenetic structure of Chinese forest tree communities.

2.1.1.2 Soil Soil properties may affect species richness and composition by both direct and resource-related effects [25]. Strong association between spatial heterogeneity of soil properties and tree species distribution is reported in GTS subtropical forest even after controlling the effect of dispersal limitation [19]. In the other subtropical forest (DHS), species distribution is found to be better explained by soil variables than topography [26]. Leaf area and wood density are also predicted to be correlated with soil fertility at both species- and quadrat-level in GTS [27]. Both tree species composition and tree survival in the Changbaishan (CBS) temperate forest are found to be more controlled by soil variables than topography [28, 29]. Spatial distribution of soil organic carbon in CBS is also mainly structured by soil properties, such as soil moisture and pH [30]. In XSBN tropical forest, soil nutrients was consistently found to be a better explanatory factor than spatial distance for both phylogenetic and functional beta diversity, indicating a stronger role of deterministic environmental processes relative to stochastic dispersal-related processes in community assembly [31]. In all, soil properties in Chinese forest play important roles in shaping the species composition, functional and phylogenetic structure of its tree assemblages.

2.1.1.3 Light Understory light is an important environmental variable for tree species regeneration in forest communities, strongly affecting community composition and structure [32]. In CBS temperate forest, available understory light is positively correlated with seedling survival of shrubs and light-demanding species [33]. In GTS subtropical forest, seed rain and seed limitation showed similar patterns between community understory and gaps, indicating a neutral role of gaps in shaping seed diversity in this forest [34]. Using the ratio of light-demanding species as an indicator of light availability (also an indicator of nature disturbance), a strong relation between functional structure and proportions of light-demanding species across 11 forest plots was shown [35]. While these studies indicate that light levels within forest affect community structure, the role of light availability in shaping forest structure in China has only been studied to a limited extent, with focus mainly on tree regeneration and functional composition.

2.1.2 Biotic interactions

In addition to relations between plants and environment, interactions among con- or heterospecific plant individuals or between plants and other organisms can also be very important in community assembly, and have also received attention in CForBio, with a focus on negative density dependence [33, 36, 37].

2.1.2.1 Negative density dependence As an important mechanism in biodiversity maintenance, negative density dependence has been widely tested in the past decades [38, 39]. In the GTS subtropical forest, negative density dependence is prevalent, even after controlling the effects of habitat heterogeneity [36]. In contrast, in the other subtropical forest not far away from GTS, only evidence of negative density dependence at early life-history stages was found [40]. While the evidence of negative density dependence, as a factor in tree community assembly, has historically been reported primarily from tropical forests, CForBio has strengthened the evidence for the role of this mechanism also in forests outside the tropics. In the CBS temperate forest, tree survival is negatively related with conspecific basal area for most species, indicating the role of negative density dependence in regulating species composition [41]. Further, in the Liangshui (LS) temperate forest, negative density dependence is prevalent across multiple life stages [37]. Hence, negative density dependence is an important factor for local tree community assembly broadly across China's forests.

2.1.2.2 Mutualism Besides the negative biotic interactions, positive relations among species should also be considered in community ecology [42, 43]. However, studies on this topic in CForBio are very limited. In GTS subtropical forest, ectomycorrhizal (EM) fungi diversity is positively connected with host plant diversity, with genus-level plant diversity being a better predictor than species- and family-level diversity [44].

2.1.3 Local dispersal

Neutral theory of biodiversity assumes that every species is ecologically equivalent and dispersal limitation is the main force structuring community patterns [45]. Most studies in CForBio that tested this hypothesis have used spatial distance as a surrogate of dispersal limitation and found that dispersal limitation plays important roles in shaping species, functional and phylogenetic diversity patterns [31, 46, 47]. In the CBS temperate forest, Jaccard coefficients between seed rain and neighboring adult trees significantly decrease with an increasing neighborhood radius, indicating the role of dispersal limitation in this forest [48]. The few other studies on seed rain and seed limitation only provide descriptive information about the phenology, syndromes and distributions of tree species in different habitats in GTS subtropical forest [34, 49].

2.1.4 Human impacts

Forest is one of the ecosystems that have been most affected by human activities in China [7, 11]. The influence of human activities on Chinese forests has also been examined in CForBio. In DLS temperate forest, ground beetles show a higher species richness in naturally regenerated remixed forest than in other monoculture forests [50]. Different forest management histories in GTS also have strong effects on tree community phylogenetic and functional structure, with a less clustering structure in more mature forest, and thus may affect forest ecosystem functioning via diversity effects [51], i.e., in addition to effects on stand age and structure.

2.1.5 Interaction of local factors

An increasing number of studies have emphasized the necessity of considering multiple factors simultaneously to explain biodiversity patterns, notably to quantify the relative importance of biotic and abiotic processes or their interactions [46, 52].

In the GTS subtropical forest, variation in species richness (~53 %) and composition (~65 %) were jointly explained by habitat and space, and the relative roles of these two processes change with spatial scales, with neutral processes (43 % variation explained) more important than environmental control (20 %) at fine scale [46]. Seedling dynamics in this forest as well as in the CBS temperate forest are affected by both density dependence and habitat associations [52, 53]. The spatial distribution of tree species in the DHS subtropical forest suggests that seed dispersal limitation, competition and habitat heterogeneity together affect species coexistence [54]. In the CBS temperate forest, environmental filtering is more important at broader scale, while biotic interactions are more important at finer scale, with a reduced importance of both factors at very fine scales, possibly reflecting an increased importance of non-spatial stochastic dynamics, e.g., demographic stochasticity [28]. Genetic structure of *C. chinensis* in DHS subtropical forest is linked to both topography and species life-history traits, such as pollination and dispersal, which lead to a higher genetic diversity in windward ridges [23].

2.2 Regional factors

In the last decades, evidences have accumulated for the importance of large-scale processes for local community assembly [15, 16]. In the case of China's forests, historical climate change together with contemporary climate were linked with species richness in Chinese mountain forests [55]. Regional species richness also significantly affected local species richness in Chinese forests [56]. Widely distributed glacial refuge during Quaternary in China has also left strong genetic imprints in China's diverse temperate flora [57].

However, so far most studies in CForBio have focused on local factors, with only a few addressing the role of regional processes [35, 58]. By linking phylogenetic and functional structure in Chinese forests to current and glacial climate as well as local disturbance, the glacial–interglacial shift in temperature is found to be the strongest explanatory factor for phylogenetic structure, with more overdispersed structure in areas with stable climate, supporting the niche conservatism hypothesis [35]. In contrast, local disturbance emerged as the factor having the strongest explanatory power for functional community structure, with more clustered structure in more disturbed forests [35]. Also, when expanding the species pool from East Asian to a global scale, forest communities in East Asia have lower Net Relatedness Index (mainly reflecting the basal phylogenetic structure) and higher Nearest Taxon Index (reflecting the tip phylogenetic structure), indicating the role of inter-continental migration, climatic conservatism, as well as local diversification in shaping the geographic variation in phylogenetic structure of these forests [58].

3 Perspectives

Forests harbor high levels of biodiversity at multiple trophic levels or different groups, not only woody plants.

An intact forest ecosystem includes woody plants, herbs, bacteria, fungi, insects, birds, mammals, etc. All of these components have direct or indirect connections through competition, facilitation, parasitism, predation, and so on. Factors affecting these components and connections not only include local environment and biotic interactions, but also increasingly include a range of anthropogenic global change factors, notably human-induced climate change, direct effects of increasing human populations, invasive species and defaunation.

CForBio includes 13 large permanent forest plots across eastern China along a latitudinal gradient from tropical and subtropical, through temperate, to boreal areas [14], whereas the research conducted at CForBio and has published so far has not yet linked all these plots together to address the divergence in biodiversity and forest ecosystems across these climatic zones. It would be much powerful to conduct coordinated well-designed common analyses and experiments across these plots to study and disentangle the effects of paleo- and contemporary climate, evolutionary dynamics, species invasions and human activities on the biodiversity and ecosystem services of China's forests.

3.1 Organism groups beyond woody plants

So far, most publications in CForBio only focused on diversity patterns and community structure of woody plants. However, other groups of organisms also exist and interact with each other in the diverse forest ecosystem. For instance, herb-layer diversity and biomass are important component of forest ecosystem [59, 60]. Notably, density and distribution of tree seedlings may be strongly affected by herb patches [59]. Herbaceous diversity and biomass can also be correlated with tree-layer diversity [60]. Moreover, different tree species could have distinct microbial communities, including bacteria, fungi and archaea [61]. On the other hand, microbes may also have a range of effects on plant communities, in terms of diversity, structure and productivity [62].

Furthermore, tree diversity, composition as well as tree cover could affect both underground and aboveground animal diversity [63–65]. For instance, in a Central European deciduous forest, earthworm densities are positively correlated with tree species diversity, indicating the important role of diverse food qualities for decomposer fauna [64]. Diversity and composition of tree communities could also affect herbivory diversity, providing evidence for the role of biodiversity in maintaining ecosystem functioning across different trophic levels [65]. Tree cover in agricultural landscapes could significantly affect diversity of birds, bats, butterflies and dung beetles [63].

To sum up, forest is a high diverse ecosystem composed of many different groups of organisms and these groups have very complex direct and indirect interactions, e.g. like a network [66], thus it is of crucial importance to consider these different groups and their interactions when study the mechanisms underlying forest biodiversity and functioning in CForBio.

3.2 Defaunation

Diversity of animals strongly shape species composition, structure and functioning of tree communities [67, 68]. In Congo tropical forest, seed dispersal and recruitment of trees with megafaunal syndrome are significantly affected by the number of elephant [67]. In a Spanish temperate secondary forest, all components of seed dispersal (both number and richness of dispersed seeds) are positively related with richness of frugivorous birds [68].

Defaunation, the decline or loss of large and medium native vertebrate populations, has affected the forest biome a lot, with an effect even larger than deforestation and logging combined [69, 70]. The consequence of defaunation on forest biodiversity, structure and functioning has been well documented [70, 71]. For instance, empty forest resulted from defaunation is widely distributed in China, even in its nature reserves [72, 73]. Local tree diversity is consistently declining over 15 years in a tropical forest community (a large permanent forest plot) because of overhunting [70]. Seed size in palm populations in Brazilian Atlantic forest is smaller in areas without their large avian frugivores than in non-defaunated regions [74]. Carbon storage is significantly influenced by defaunaion of large frugivores in 31 Atlantic forest communities [71]. However, so far, no studies in CForBio has investigated effects of defaunation on the composition, structure and functioning of Chinese forests.

3.3 Climate change

One of the important ecosystem service provided by forest is its influence on climate through biological, physical and chemical processes. However, most studies in the past decades have focused on the opposite influence, i.e., the influence of climate change on forest ecosystems [2]. One of the reasons why China has more diverse forest types and composition than North America and Europe is that China has been relatively less affected by the glacial–interglacial climate change [7]. Nevertheless, in the past century and in the future, climate change has and will significantly influence the composition, structure, distribution and functioning of Chinese forests [75].

For instance, regional-scale drying in the past 34 years is probably responsible for the reorganization of China's tropical and subtropical forest, e.g., increasing numbers of individuals and species for shrubs and small trees but decreasing numbers of individuals and species of trees [76]. Studies based on permanent plots in American and African tropical forest also show that increased drought strongly affected the species richness, functional composition as well as ecosystem functioning [77, 78].

A dominant effect of climate warming on temperate forest in north-eastern China is evident only in high and low elevations areas, not in areas with mid-elevation, suggesting that the southern and northern edges of forest ecosystem are more vulnerable to climate change [79]. In addition to these leading edge and trailing edge changes, climate change effect on species range shifts should also consider the optimum position or the abundance changes [80]. Moreover, globally speaking, research efforts on climate-related range shifts in China are relatively weak, especially in the subtropical and tropical biomes [80]. Therefore, the CForBio network provides an important chance to improve the geographic shortfalls of climate-related range shifts research.

Except for these direct effects, climate change could also indirectly affect forest composition and structure by influencing the distribution and abundance of forest insects, pathogens and fire [81–83]. In a boreal forest in Northeast China, spatial distribution of fire occurrences is strongly affected by climatic change and human influence [81]. Actually, forest fire is one of the major drivers of forest dynamics in the circumpolar boreal region [82]. In contrast, biotic disturbances by insects and diseases are strongly influencing forest composition and structure at a global scale [83, 84].

One of the main purposes of CForBio is to monitor the long-term change of forest biodiversity and structure. However, so far few CForBio studies have investigated the effects of contemporary climate change. Moreover, because the ecosystems in western and northern China are more sensitive to climate change than ecosystems in East China [75], and the current distribution of forest plots in CForBio concentrated in East China [14], it is very important to have more long-term monitored large forest plots in these regions, especially the western part, to better understand the effect of climate change on Chinese forests.

3.4 Remote sensing

The area of forest on the Earth is four billion hectares, about 30 % of its total land area [85]. Thus, to better understand the change of forest composition and structure at various spatial scales, it is impossible to only rely on forest inventory. Based on Earth observation satellite data, forest cover changes between 2000 and 2012 were analyzed globally at a spatial resolution of 30 meters [86]. Spatially implicit information from aerial images (7 cm pixel^{-1}) of canopy gaps produced by unmanned aerial vehicles could assess plant diversity of forest understory very well ($R^2 = 0.74$) [87]. Also using unmanned aerial vehicles, remote sensing based canopy height, above-ground biomass, percent canopy openness, as well as predicted frugivore presence and abundance were strongly correlated with field-based measures [88].

At this point, CForBio already has 13 large permanent forest plots, but this is still not enough to represent all forested areas in China. To better understand and conserve forest biodiversity, combine remote sensing with plots investigation is quite useful and necessary.

4 Conclusion

The CForBio is an important network for monitoring and investigating biodiversity patterns and dynamics as well as the underlying mechanisms in China, a fast developing country with large population and rich biodiversity. This synthesis of the research conducted in CForBio shows that strong progress in understanding the patterns of biodiversity and community structures and the drivers for their changes in the forests of different climatic zones has been achieved. More efforts should be put, first, to conduct coordinated and well-designed common experiments in different forest ecosystems along the latitudinal gradient, so as to reveal the effects of large-scale drivers as historical and contemporary climate on the biodiversity and ecology of the forests in China; second, the CForBio should extend its research from forest plant communities to forest ecosystems, that is, to study the organisms in forest and their interactions and relations with environment for a better understanding of the drivers and processes responsible for forest dynamics and community assemblage and biodiversity loss.

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

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