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Effects of canopy and understory nitrogen addition on the structure and eco-exergy of a subtropical forest community

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ABSTRACT

The health of plant communities has been severely threatened by nitrogen (N) deposition across all types of ecosystems. The effect of N deposition on the structure of forest communities (as measured by the Shannon Wiener index, evenness, richness, density and biomass) has been investigated extensively, mostly through understory N-addition experiments, which has been criticized for neglecting the function of the canopy in interception, up-take and transformation of N, as well as other elements. To clarify this problem, the effects of canopy and understory N-addition on subtropical evergreen forest community structure were quantified and compared in this study. Furthermore, a bio-thermodynamic measurement, eco-exergy, was applied as a complement to the classic community structure index system to evaluate the health status of forest communities by bringing the genetic information embodied in each species into consideration. The results showed that compared to understory N-addition, richness in the shrub layer was more sensitive to the canopy N-addition. Thus, studies that only consider the effects of N-addition to the understory may underestimate the effects of N-addition on forest communities, as a whole. In this study, even though N-addition to the understory did not alter the forest structure indices (Shannon Wiener index, evenness, richness, density and biomass), significantly, it did decrease the specific eco-exergy of the subtropical, evergreen, forest community, as observed for N-addition to the canopy. The decrease was mainly contributed by the decline in the fraction of higher plants and an increase in the fraction of lower plants within the tree and herb layers. Thus, our results demonstrated that the health status of the subtropical, evergreen, forest community as determined by thermodynamic measures was more sensitive to N-addition compared to the classic community indices mentioned above, and the community structures in both tree and herb layers were also sensitive to N-addition, besides the shrub layer.

1. Introduction

Annual global atmospheric nitrogen (N) deposition increased over 12 times from 15 Tg N in 1860 to 187 Tg N in 2005 and is predicted to reach 200 Tg N yr^{-1} by 2050, due to the continued increase in the combustion of fossil fuels, growing demand for N in agriculture and industrial production (Galloway et al., 2008). Tropical and subtropical regions have received substantial N deposition in the past decades, and the increasing trend of N deposition is unlikely to be changed soon (Galloway et al., 2008; Richter et al., 2005). Studies on the effects of N deposition on ecosystems have been focused on the temperate and boreal forests, while few research studies have been conducted in subtropical forests (Bobbink et al., 2010; Galloway et al., 2008).

Previous studies about the effects of nitrogen addition (N-addition) on forests, including a few recent studies on subtropical forests, were mainly based on understory N-addition experiments (Avolio et al., 2014; Lu et al., 2010; Lu et al., 2018; Lu et al., 2011b; Mao et al., 2017; Talhelm et al., 2013; Wu et al., 2013). However, there is still a debate about whether adding N to understories directly can realistically simulate the effects of atmospheric N deposition on forests, since the function of the canopy in interception, up-take and transformation of the deposited N and other elements and compounds is not considered. Results from many studies in forest ecosystems have shown that the canopy takes up and transforms deposited N through leaves (Wortman et al., 2012), epiphytes (lichen, cyanobacteria) (Gaige et al., 2007; Lindo and Whiteley, 2011) and micro-organisms (Cape et al., 2010). It

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has been shown that about 30–85% of N deposition is intercepted by the canopy and that retention is higher for NH_4^+ than for NO_3^-, with the rates of uptake varying among different forests (Chiwa et al., 2004; Houle et al., 2015; Tomaszewski et al., 2003). Studies from southeast China showed that about 30–50% of the N deposited was retained by the canopies of *Castanea. henryi* and other dominant tree species, and the canopy leaf nitrogen content of *Castanea. henryi* increased by 20% after two years of N-additions (Liu et al., 2018b). Furthermore, canopy uptake and assimilation of atmospherically deposited N by leaves have effects on the tracheid size of dominant species (Jiang et al., 2018), photosynthetic performance (Liu et al., 2018a) and net ecosystem CO_2 exchange (Sievering et al., 2017). All three of these factors indicated a possibly different effect of canopy and understory N-addition on forest structures and functions.

The effects of N deposition on the forest community, especially on biodiversity (Shannon Wiener index, evenness, density, richness and coverage), have received wide interest, with still no consensus on the results (Avolio et al., 2014; Gilliam et al., 2016; Lu et al., 2011b; Smith et al., 2016; Wu et al., 2013). Some studies showed that N-addition significantly decreased the biodiversity of understory and groundcover species in boreal and temperate forests (Gilliam et al., 2016; Talhelm et al., 2013), while some other researchers reported that N-addition increased (Strengbom et al., 2002) or had no significant effects on biodiversity due to the species-specific and high background levels of N deposition (Gillian et al., 2006; Bobbink et al., 2010). Also, the effects of N-addition on biodiversity are different in the subtropical forests at different succession levels, e.g. 5-years of N-addition significantly decreased the understory richness and density in an old-growth forest (Lu et al., 2010), but the effects were not significant in disturbed or rehabilitated forests (Lu et al., 2011b). In other studies, the effects of N-addition on different functional groups have been explored (Avolio et al., 2014; Bai et al., 2010; Lu et al., 2010; Stevens et al., 2010). A functional group is defined as a set of plants exhibiting a similar response to the environment and having the same effects on ecosystem processes (Chapin et al., 1996). Although these earlier studies have focused on the functional group, they still lack an intrinsic connection with species. No universal effect of N-addition on the forest community has been found yet; however, different effects were found on different types of forests and plants belonging to different layers and physiological groups within the forest.

All ecological processes are accompanied by energy transformation, and all follow thermodynamic laws (Jorgensen, 2002; Odum, 1995). Thus, there may exist a common thermodynamic effect resulting from N-addition to forest communities, behind the complicated effects of N-addition on different plants and communities. First put forward by Mejer and Jørgensen at the end of the 1970s, eco-exergy is defined as the free energy of all biotic composition in an ecosystem, and it is calculated as a multiplication of the biomass and the information embedded in the genetic complexity of species (Mejer and Jørgensen, 1979). By taking the evolutionary status and genetic information of different species into account, eco-exergy can be applied as a complement to the classic community structure index system, which generally includes biomass, richness, and other diversity indices etc., without considering the evolutionary status and embodied genetic information in different species. On one hand, since eco-exergy has a clear biophysical meaning, i.e. it is the distance of the genetic structure from thermodynamic equilibrium, eco-exergy has been widely used as an indicator of the self-organization/development and health status of communities and ecosystems (Jorgensen and Nielsen, 2007). On the other hand, the specific eco-exergy is defined as the eco-exergy divided by the biomass and it expresses the dominance of the higher organisms, because per unit of biomass they carry more information, that is, they have higher β-values (Jørgensen, 2000). Some ecosystems have a high eco-exergy due to large biomass, but a low specific eco-exergy, because the biomass is dominated by lower species with low β-values. The combination of the eco-exergy and specific eco-exergy indices usually gives a more satisfactory description of the health of an ecosystem than the eco-exergy index alone, because it considers diversity and life conditions for higher organisms (Jørgensen, 2000). The eco-exergy theory was initially applied in assessing the effects of disturbance on the health of aquatic and wetland ecosystems, including those altered by biological invasion (Chen et al., 2018b), eutrophication (Marques et al., 1997) and abiotic factors (Wang et al., 2017). Recent studies confirmed that eco-exergy and specific eco-exergy can be used as a complement to the classic community structure index system for indicating the succession or degradation of not only aquatic systems and wetlands, but also forests (Chen et al., 2018b,c; Huang, 2012; Lu et al., 2015, 2011a; Molozzi et al., 2013). Previous studies explored the specific eco-exergy and species diversity of the subtropical, evergreen, broad-leaved forest community, as indicated by the Shannon Wiener index and the Simpson and Pielou index, which were much more sensitive to the disturbance of urbanization, compared with eco-exergy and biomass (Huang, 2012). However, the effect of nitrogen deposition on the thermodynamic structure of forest ecosystems has not been disclosed yet.

The maximum empower/eco-exergy principles (Odum, 1995; Jørgensen and Mejer, 1977) have been confirmed in the development of subtropical forest plantations, i.e. the eco-exergy of forest communities continued to increase with forest development, primarily through the accumulation of biomass, and then by the increase of biodiversity indicated by species richness and specific eco-exergy (Lu et al., 2015). From another perspective, a hierarchical response framework was proposed by Smith, Knapp and Collins, i.e., after relatively rapid individual level (physiological/metabolic, mortality) responses, the species in the communities will reorder because of some species being favored by changing conditions at the expense of others, which ultimately results in large changes in the community structures and functions (Smith et al., 2009). Based on the maximum empower/eco-exergy principles and the hierarchical response framework, in this study, we hypothesize that the degradation of the forest communities can be divided into three steps: The species composition will change at first, some higher species being replaced by lower species. Then, the community diversity will decrease. The community biomass will decrease finally, in response to disturbance. The purpose of this study was to: (1) quantify and compare the effects of N-addition methods and concentrations on the plant community structure of subtropical forests and their eco-exergy based on a healthy thermodynamic status; (2) combine the classic structure indices with eco-exergy to study the effects of N-addition on the structure of the subtropical forest community.

2. Materials and methods

2.1. Study site

This study was conducted in Shimentai National Nature Reserve (24°22′-24°31′ N, 113°05′-113°31′ E), Guangdong Province, South China. The reserve is located in the transitional zone from the southern subtropics to the central tropics and has a subtropical monsoon climate, which is covered by a broad-leave, evergreen forest. The mean annual temperature is 20.9 °C, with an average coldest month (January) and warmest month (July) temperature of 10.9 °C and 28.9 °C, respectively. The mean annual rainfall of 2364 mm is distributed seasonally, with 71% of it falling from April to September and 29% falling from October to March. Nitrogen deposition in rainfall in Shimentai National Nature Reserve was 34.1 kg N ha^{-1} yr^{-1} (Zhang et al., 2015).

2.2. Experimental treatments

The N-addition experiments were initiated in April 2013, and the initial vegetation data was collected before the first treatment. A total of twenty 20 m × 20 m plots were established, corresponding to five treatments and four replicates. The treatments include a Control without treatment (CT), canopy N-addition 25 kg N ha^{-1} yr^{-1} (CN25),

canopy N-addition 50 kg N ha^{-1} yr^{-1} (CN50), understory N-addition 25 kg N ha^{-1} yr^{-1} (UN25), understory N-addition 50 kg N ha^{-1} yr^{-1} (UN50). All treatments were laid out randomly in each block. The canopy spraying system consisted of five components: a tank for storing N solution, connecting pipes, a supporting tower, four sprinklers and a central computer controller, which was built at the center of the canopy of the N-addition plot. An automatic irrigation system with a height of 1.5 m was applied in each understory N-addition plot. Each plot was surrounded by a 20 m buffer strip to minimize the contamination between adjacent plots. During each application, ammonium nitrate, NH_4NO_3, was weighed and mixed with water at different concentrations. Application of NH_4NO_3 solution was administered once a month from April to October. The total addition of solution was 21 mm per year, accounting for < 1% of the total annual precipitation of the forest site, so the confounding effect caused by the addition of water was negligible (Zhang et al., 2015).

2.3. Experimental methods

2.3.1. Vegetation survey

The vegetation survey was conducted in December 2017, after four years of N-addition treatments. A 100 m^2 quadrat for trees, a 25 m^2 quadrat for shrubs, and a 1 m^2 quadrat for herbs were set up in each plot. The tree layer is defined as diameter at breast height (DBH) ≥ 1 cm, and the shrub layer is described as DBH < 1 cm. Herbaceous plants, woody vines and ferns were classified into the herb layer. The height, DBH and crown width were measured for trees, and the height, stem diameter and crown width were surveyed for shrubs, and the height and coverage were measured for herbs.

2.3.2. Shannon Wiener index, evenness, richness, density and biomass

The classic structure indices included the Shannon Wiener index, evenness, richness, density and biomass. The Shannon Wiener index (H) was calculated as:

$$H = -\sum (p_i \ln p_i)$$

where p_i is the ratio of the number of the *i*th species to the total number of all species in each plot.

The evenness (E_H) was calculated as:

$$E_H = H/\ln(S)$$

where S is the total number of species in each plot.

The species richness was recorded as the number of species m^{-2} in each replication, and the individual density was the number of plants m^{-2} in each replication. The calculation of biomass in the tree and shrub layers refers to the same species growth equation in the Dinghushan and Heshan National Nature Reserve, Guangdong Province, South China (Chen et al., 2015). For those species without growth equations, the growth equation for the genus or family that they belonged to was employed, and the biomass prediction model was applied (Wen and Wei, 1997; Yang and Guan, 2007).

2.3.3. Eco-exergy calculation

The following formulas were applied to calculate eco-exergy.

$$E_X = 18.7\text{kJ/g} \times \sum_{i=0}^{n} C_i\beta_i$$

where 18.7 kJ/g is the mean eco-exergy of detritus or dead organic matter; C_i is the biomass of the *ith* species (g/m^2); β_i is the weighting factor of the *ith* species relative to detritus (Jorgensen et al., 1995; Lu et al., 2011a).

$$\beta = 1 + \frac{\ln(20^{1.65\times10^8 C})}{7.43} \times 10^5$$

where the C-value is the amount of DNA in the haploid nucleus of the plant cell, which was obtained from the Plant DNA C-values Database of the Royal Botanic Gardens, Kew, UK (Fonseca et al., 2000). For those species without C-values, the mean C-value for the same genus or family was applied.

The specific eco-exergy was calculated as:

$$SpE_{X=}\left(18.7kj/g \times \sum_{i=0}^{n} C_i\beta_i\right) / \sum_{i=0}^{n} C_i$$

where all factors and variables (C_i and β_i) are defined in the same manner as those in eco-exergy equation.

2.3.4. Community similarity index

The similarity index (Sj) is based on the Jaccard distance. The following formula was applied to calculate similarity index.

$$S_j = \frac{c}{a + b - c}$$

where a and b are the number of species in two communities, and c is the number of common species in the two communities. 0 ≤ Sj < 0.25, extreme dissimilarity; 0.25 ≤ Sj < 0.50, medium dissimilarity; 0.50 ≤ Sj < 0.75, medium similarity; 0.75 ≤ Sj < 1, extreme similarity.

2.3.5. Data analysis

One-way ANOVA with Tukey's honest significant difference (HSD) test was performed to compare the effects of the methods and the concentrations of N-addition on the Shannon Wiener index, evenness, richness density, biomass, eco-exergy and specific eco-exergy. Before the treatments started in 2013, the vegetation of the experimental site was homogenous, with no significant difference between the control and N treatment plots for any measured variables (Table A1). Data analyses were carried out by R version 3.3.1 using the package vegan and the package dplyr. Statistically significant differences were set at $P < 0.05$.

3. Results

3.1. Effects of N-addition concentrations and methods on the plant community structures

3.1.1. N-addition concentrations

One-way ANOVA showed that the concentrations of the N-addition had no statistically significant effects on the usual community structure indices, i.e. Shannon Wiener index, evenness, richness, density and biomass (Fig. 1).

The N-addition concentrations applied did not significantly change the community structure indices in the different layers, except for the shrub richness when N was added to the canopy (Fig. 1). The richness in the shrub layer receiving 25 kg N ha^{-1} yr^{-1} through canopy N-addition was significantly higher than shrub layer species richness, when receiving 50 kg N ha^{-1} yr^{-1} through addition of N to the canopy, although neither one was significantly different from the control (Fig. 1e).

3.1.2. N-addition methods

One-way ANOVA showed that neither N-addition method significantly altered the community structure indices, i.e. Shannon Wiener index, evenness, richness, density and biomass (Fig. 2).

Except for richness in the shrub layer, the effects of N-addition method on the other structural indices were not significant for any of the three layers. The value of the richness with canopy N-addition 25 kg N ha^{-1} yr^{-1} was significantly higher than that with understory N-addition 25 kg N ha^{-1} yr^{-1} (Fig. 2e).

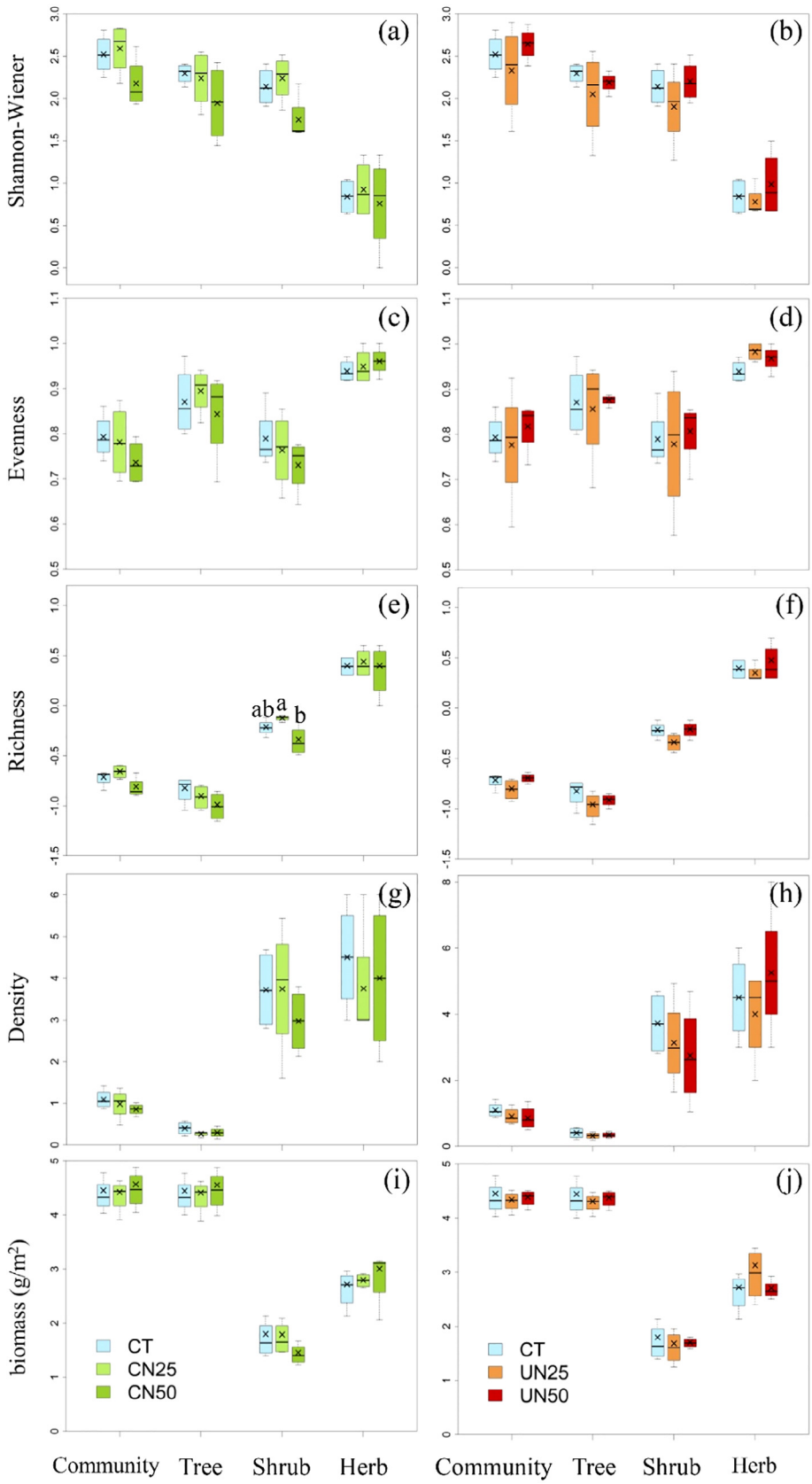

Fig. 1. Effects of N-addition concentrations on the structure of the forest community and on the plant layers within the forest: Shannon-Wiener (a, b), evenness (c, d), richness (e, f), density (g, h) and biomass (i, j) values for the community and in the tree, shrub and herb layers. Notes: Logarithmic transformation was applied to the richness and biomass measures. CT, without N-addition; CN25, canopy addition of 25 kg N ha^{-1} yr^{-1}; CN50, canopy addition of 50 kg N ha^{-1} yr^{-1}; UN25, understory addition of 25 kg N ha^{-1} yr^{-1}; UN50, understory addition of 50 kg N ha^{-1} yr^{-1}, where × is the mean of each group. The differences of group means were tested with Tukey's HSD test. The different lowercase letters indicate significant differences at $P < 0.05$ level among different treatments. The following figures use the same definitions for the treatments considered.

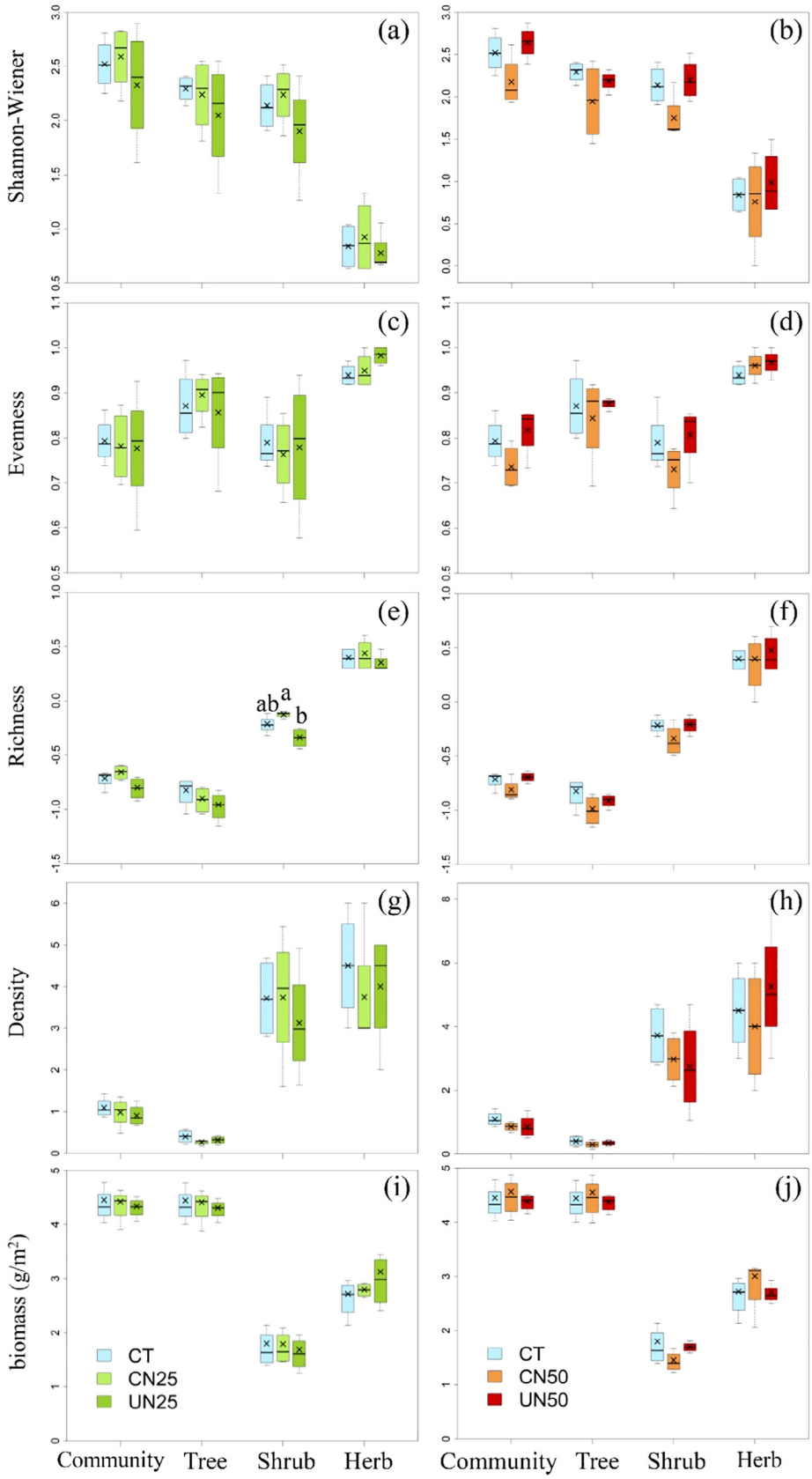

Fig. 2. Effects of the N-addition methods on the structure of the forest community and on the plant layers within the forest: Shannon-Wiener (a, b), evenness (c, d), richness (e, f), density (g, h) and biomass (i, j) values for the community and in the tree, shrub and herb layers.

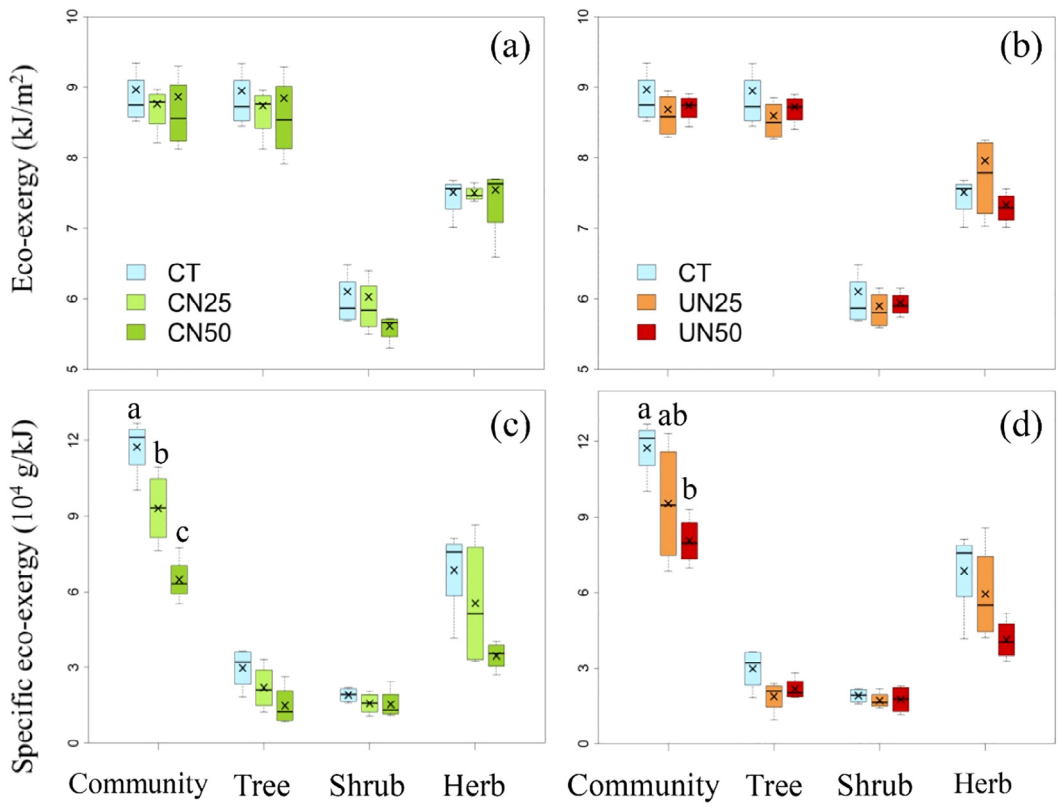

Fig. 3. Effects of N-addition concentrations on the plant eco-exergy (a, b) and specific eco-exergy (c, d) of the community and in the tree, shrub and herb layers.

3.2. Effects of N-addition concentrations and methods on the eco-exergy and specific eco-exergy

3.2.1. N-addition concentrations

In most cases, the eco-exergy and specific eco-exergy of the forest community showed a declining trend under the N-addition treatments, compared to the control (Fig. 3). One-way ANOVA showed that the concentrations of N-addition had significant effects on the specific eco-exergy of the forest community, but no significant effects on the eco-exergy (Fig. 3). Both 50 kg N ha^{-1} yr^{-1} additions to the canopy and understory significantly decreased the specific eco-exergy of the community compared to the control, while only the 25 kg N ha^{-1} yr^{-1}N-addition to the canopy significantly decreased the specific eco-exergy of the community relative to the control.

None of the N-addition treatments significantly altered the eco-exergy or the specific eco-exergy of the three different layers. The eco-exergy and specific eco-exergy of the different layers showed decreasing trends relative to the control, except for the eco-exergy in the herb layer (Fig. 3).

3.2.2. N-addition methods

One-way ANOVA showed that the N-addition methods had no significant effects on the communities' eco-exergy (Fig. 4a and b). However, the effects of N-addition methods on the communities' specific eco-exergy became significant for the 50 kg N ha^{-1} yr^{-1} treatments compared to the control (Fig. 4d).

Similarly, the effects of N-addition methods on the different layers were mainly reflected in the specific eco-exergy of the 50 kg N ha^{-1} yr^{-1} treatments. In the tree layer, canopy addition of 50 kg N ha^{-1} yr^{-1} decreased the specific eco-exergy relative to the control, but the effect was not significant for understory addition at 50 kg N ha^{-1} yr^{-1}. In the herb layer, canopy and understory additions of 50 kg N ha^{-1} yr^{-1} decreased the specific eco-exergy relative to the control. In general, the specific eco-exergy in the tree and herb layers was more sensitive to the method of N-addition than that in the shrub layer (Fig. 4).

3.2.3. Community similarity index

The community similarity indices ranged from 0.24 to 0.39 (Table 1). In other words, N-addition resulted in the development of medium to extreme dissimilarity relative to the control.

4. Discussion

Our results demonstrated that the specific eco-exergy of the community declined by between 19% and 45% relative to the Control; however, no significant effects of understory N-addition on the community structure indices (Shannon Wiener index, evenness, density, richness and biomass) were observed. The results are similar to recent studies in mangrove wetlands, which have shown exotic invasion reduced both microbenthic faunal biomass and eco-exergy but had no significant effects on the Shannon Wiener index, Simpson's diversity, richness and evenness (Chen et al., 2018a,b). Studies in the subtropical forest have confirmed forest ecosystems with relatively high eco-exergy are well-developed mature systems, and they have revealed that the eco-exergy and specific eco-exergy do not develop synchronously in a linear manner (Lu et al., 2015, 2011a). Our study indicates that N-addition is harmful to the thermodynamic health of subtropical forest communities, and the eco-exergy/specific eco-exergy of the subtropical forest is more sensitive to disturbance than is indicated by the classic community structure indices, i.e. Shannon Wiener index, evenness, density, richness and biomass.

Moreover, our study showed that the community similarity index was lower than 0.5 and that the average C-value of the plant community also showed a decreasing trend (Table 2), in response to N-addition. The more common species between the communities generally have the greater similarity index; and C-value is the amount of DNA in the haploid nucleus of the plant cell, which indicates the status at the

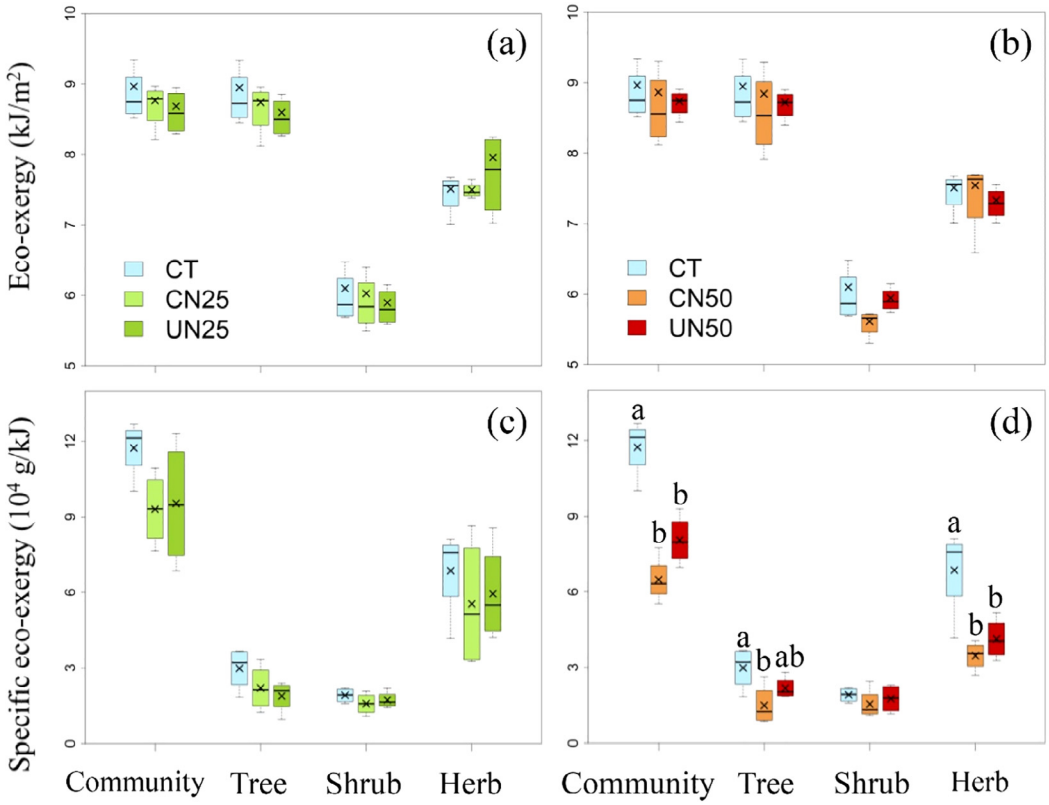

Fig. 4. Effects of N-addition methods on the plant eco-exergy (a, b) and specific eco-exergy (c, d) of the community and on the tree, shrub and herb layers.

Table 1
Similarity index (J) of the plant community under N-addition to the canopy and understory.

	CT	CN25	CN50	UN25	UN50
CT	1.00	0.37	0.34	0.35	0.39
CN25		1.00	0.30	0.33	0.31
CN50			1.00	0.24	0.36
UN25				1.00	0.35
UN50					1.00

Notes: CT, Control; CN25, 25 kg N ha^{-1} yr^{-1} with canopy N-addition; CN50, 50 kg N ha^{-1} yr^{-1} with canopy N-addition; UN25, 25 kg N ha^{-1} yr^{-1} with understory N-addition; UN50, 50 kg N ha^{-1} yr^{-1} with understory N-addition. The following table uses the same definitions for the treatments considered.

Table 2
Average C-value of the plant community under the canopy and understory N-addition.

	CT	CN25	CN50	UN25	UN50
C-value	2.05	2.15	1.99	2.02	1.94

evolutionary level. Therefore, our results disclosed that the species composition of the community changed greatly, which is reflected by the decreasing abundance of higher plants and the increasing abundance of lower plants. Another study in the subtropical evergreen broad-leaved forest community, also found the specific eco-exergy fell between 31% and 54% in response to urbanization, and communities in urban areas are composed of low C-value species (Huang, 2012).

After four years of treatment, the addition of N to the canopy had a significant effect on the shrub species richness, while the effect was not significant for N-addition to the understory (Fig. 1e; 1f). The richness after the addition to the canopy of 50 kg N ha^{-1} yr^{-1} was significantly lower than for treatment with 25 kg N ha^{-1} yr^{-1}, although neither richness value was significantly different from the control. A previous study in a tropical forest found the richness of understory plants significantly decreased after 5 years of the addition of 50 kg N ha^{-1} yr^{-1} to the understory, compared with the control (Lu et al., 2010). Another research project, conducted in the subtropical forest, has also reported that after 8 years of N-addition to the understory, plant richness of the understory was reduced relative to the control for both 12 g N m^{-2} yr^{-1} and 24 g N m^{-2} yr^{-1} treatments (Wu et al., 2013). This difference in the understory vegetation found as a result of N-addition was mainly due to the different classification used for the understory plants, as well as the concentrations and the periodicity of N-addition. In addition, these studies found that the reduction of plant diversity was largely related to changes in soil properties. However, all these previous studies are based on understory N-addition, and they neglected the important processes taking place in the forest canopy (Gaige et al., 2007; Lindo and Whiteley, 2011; Wortman et al., 2012). At our study site, research at the same location has found that canopy N treatments affect the nitrogen metabolism of woody plants, which may result in an ongoing transformation of subtropical forests into communities dominated by small trees and shrubs (Liu et al., 2018b). In contrast, N-addition has not significantly changed the soil pH (0–30 cm) at our study sites (unpublished data). Therefore, our results indicate that richness in the shrub layer is more sensitive to canopy N-addition than understory N-addition, which is mainly related to the effects of canopy N-addition on trees.

N-addition treatments significantly decreased the specific eco-exergy of the subtropical, evergreen, forest community, mainly due to the responses of the tree and herb layers (Fig. 4d). However, the effect of N-addition on richness was mainly reflected in the shrub layer (Fig. 1e), which is consistent with many reported studies of the understory or groundcover plants in boreal and tropical forests (Lu et al., 2010; Talhelm et al., 2013; Wu et al., 2013). Previous studies focused on the diversity of understory and groundcover species, due to their high sensitivity to disturbance (Gilliam, 2007; Talhelm et al., 2013). Little

attention was put on the tree and forest plant community as a whole. Recently, a study has found N-addition treatments affect the nitrogen metabolism and photosynthesis of the dominant woody plants (Liu et al., 2018b). Therefore, taking trees into consideration is necessary for a holistic assessment of the effects of N-addition on forest structure and function. Our results showed that the effects of N-addition were different in different plant layers. The different effects of N-addition on the different layers may suggest the order of disturbance or degradation, due to different sensitivities to the disturbance. At first, tree and herb species composition, based on the evolutionary level, changed; then richness significantly decreased in the shrub layer, finally the biomass showed a decreasing trend. These observations support our hypothesis that degradation due to disturbance is first reflected in species composition, then diversity, and finally biomass. However, further studies are needed to verify this hypothesis.

5. Conclusions

Addition of N to the canopy had significant effects on the richness of the shrub layer, while the effects of N-addition to the understory were not significant. Therefore, the results imply that previous studies, applying understory N-addition, may underestimate the effect of N-addition on the forest. Although understory N-addition did not significantly alter the classic indices of structure (Shannon Wiener index, evenness, richness, density and biomass), it did decrease the specific eco-exergy of the subtropical, evergreen, forest community, as did N-addition to the canopy. The decrease of specific eco-exergy in the forest community was mainly due to the decline of higher plants and the increase of lower plants within the tree and herb layers. These results indicate that the thermodynamic health of the subtropical, evergreen, forest community is much more sensitive to N-addition compared to the picture given by the classic community indices mentioned above. Furthermore, by taking community structure in the tree layer into account, instead of just focusing on the understory/groundcover plants, a comprehensive understanding of the effects of N-addition on the forest community can be attained.

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Appendix A. Supplementary data

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